CHEILOSTOMATOUS POLYZOA FROM THE UPPER BRACKLESHAM BEDS (EOCENE) OF SUSSEX

BY

ALAN HERBERT CHEETHAM, Ph.D.
Louisiana State University and University of Stockholm

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By A. H. CHEETHAM

CONTENTS

SYNOPSIS

Thirty-eight species distributed in 34 genera of Cheilostomata are identified in a collection of Polyzoa from the Upper Bracklesham Beds at Selsey, Sussex. All the species, including ten new ones and two left *nomina aperta*, are described, and several of the genera to which they belong are diagnosed. One species is re-named.

The stratigraphical and geographical ranges of the Upper Bracklesham species are compiled from the literature and are used, together with the relative abundances of colonial growth forms, to interpret the stratigraphy and palaeoecology of the Upper Bracklesham Beds and the palaeogeography of the Hampshire Basin in Late Eocene times. The morphology of the Upper Bracklesham Cheilostomata, especially their zoarial habits and the linear dimensions of their zooecia and heterozooecia, are discussed.

I. INTRODUCTION AND ACKNOWLEDGMENTS

The Eocene Polyzoan fauna of England contrasts so markedly in both abundance and diversity with that of the Continent that Vine (1889 : 156) at one time considered it doubtful that Polyzoa would ever be discovered in quantity in the British Lower Tertiaries. However, Gregory (1893), Davis (1928, 1929*a*, 1934, 1936*a*, 1936*b*, 1940, 1962), Burton (1929), and Thomas & Davis (1949) have since reported from the Eocene strata of both the London and Hampshire Basins a number of Polyzoa, including a total of 58 nominal species, with an additional 13 left *nomina aperta*, of Cheilostomata : 29 species from the London Clay, 29 species from the Lower

Bracklesham Beds, and 15 species from the Barton Beds. Only six species of Cheilostomata—*Biselenaria offa* Gregory, *Cellepora petiolus* Lonsdale, *Heterocella* sp., *Lunulites transiens* Gregory, *Poricellaria alata* d'Orbigny and *Teichopora clavata* Gregory (Lonsdale 1850, Gregory 1893, Davis 1962)—have been known to occur, heretofore, in the Upper Bracklesham Beds.

On the other hand, more than 125 nominal species, a number of them doubtless synonyms, have been identified among the Cheilostomata from the Eocene beds of the Paris Basin (Buge 1946), most of them from the Lutetian and Auversian Stages. Such characteristic French Eocene genera as *Caberoides* Canu, *Dakaria* Jullien, *Entomaria* Duvergier, *Gaudryanella* Canu, *Hippoporina* Neviani, *Kionidella* Koschinsky and *Tubucella* Canu & Bassler have not so far been reported in co-eval faunas in Britain.

In November 1961 Mr. Dennis Curry presented to the British Museum (Natural History) an unsorted collection of Polyzoa from the Upper Bracklesham Beds at Selsey, Sussex. The task of sorting and studying this collection was undertaken in December 1961 and continued intermittently through 1964. Thirty-eight species belonging to 34 genera have been identified among the Cheilostomata, and a less diversified assemblage of Cyclostomata, not treated here, awaits investigation.

This work fills a gap in the stratigraphical record of British Cheilostomata and permits fresh interpretation of the history of Anglo–Franco–Belgian Polyzoan faunas. The study has been complicated by the scattered, in many cases vague, descriptions and long synonymies of the Continental Eocene Cheilostomata and by some still controversial aspects of British–European stratigraphical correlation. The modern works of Curry (1958*a*, 1958*b*, 1962, 1962 MS.), Davis & Elliott (1957), and Wrigley & Davis (1937), which have especially promoted understanding the British Lower Tertiaries and their relation to those of the Continent, have proved indispensable to the compilation and interpretation of the stratigraphical ranges of the Upper Bracklesham species.

Taxonomic distinctions between the Upper Bracklesham species are in general clear ; generic relationships are in some cases not so clear. Some of the species are almost exactly intermediate between genera, the more modern representatives of which are separated by definite morphological gaps ; others do not fit properly into any known genus. Still another source of difficulty is the confusion arising from mis-application of generic names, as in the case of *Vincularia* Defrance. As a taxonomic expedient, provisional assignment to named genera has been preferred to the institution of new, in most cases monotypical, genera.

The main part of this study was carried out in the British Museum (Natural History) and at Louisiana State University. The biometrical analyses were completed at the University of Stockholm.

I am grateful to the Keeper of Zoology, British Museum (Natural History), for the use of research facilities and specimens in his care ; to the Keeper of Palaeontology for permission to continue working with the Curry Collection after my return to Louisiana State University, as well as to examine other specimens, including the H. Milne Edwards, J. W. Gregory, and A. G. Davis Collections, in his care ; to the

Geology Department, Louisiana State University, for use of research facilities and for financial support for illustrations ; and to the Geological Institute, the University of Stockholm, for the use of research facilities.

Dr. Anna B. Hastings and Dr. H. Dighton Thomas have been extraordinarily generous in guiding me through the many problems—taxonomic, nomenclatorial, and phylogenetic—which have arisen during the course of the study. It is impossible to express strongly enough my warm appreciation of their help and encouragement. Miss P. L. Cook has also given valuable advice on taxonomic problems as well as help in locating specimens and references. Others of the British Museum (Natural History) staff, including Miss S. A. Clark, Mr. R. F. Wise, and Mr. P. J. Hayward, have rendered competent technical assistance for which I am very grateful.

Mrs. Martha M. Deboo, formerly of Louisiana State University, prepared the illustrations. Her assistance has contributed greatly and essentially to the completion of this work.

Mr. Dennis Curry has generously supplied additional material from the Upper Bracklesham Beds at Selsey and samples of the Barton Beds at Barton, Hants, and of the Sables de Fresville (Lutetian) at Gourbesville (Manche), France, from which specimens of Polyzoa were obtained for important comparisons. Dr. Sten Schager of the University of Stockholm provided Rumanian Eocene material which has proved equally important for comparisons.

The National Science Foundation, U.S.A. (through a post-doctoral fellowship in 1961–62), Louisiana State University, and the Chancellor of the Swedish Universities (through a visiting professorship in 1964–65) have all made this research possible.

II. STRATIGRAPHY AND PALAEOGEOGRAPHY

The Curry Collection of Polyzoa was made from the well-known outcrop of the Bracklesham Beds in Bracklesham Bay, at Selsey, Sussex (National Grid, SZ 845926 ; Curry 1958*b* : 34). The exposures, on the foreshore, " are not so good as once they were and so much depends upon the chances of wind and tide that further detailed collecting there requires the complete leisure of a local resident " (Wrigley 1934 : 1).

Though the Bracklesham Beds at Selsey had been studied earlier by Dixon (1850), Fisher (1862) was the first to record the details of their stratigraphy. At Bracklesham Bay, Sussex, and at Whitecliff Bay, Isle of Wight, he recognized four fossil zones (A–D) which comprise alternating beds of glauconitic, shelly sand and sandy clay, " the clays being more prevalent in the highest member, and sands in the lower " (Fisher 1862 : 67). The three lower divisions (B–D) have since been assigned to the Lutetian and Cuisian Stages of the Continental Eocene on the evidence of their larger Foraminifera, *Nummulites laevigatus* (Bruguière) and *N. planulatus* (Lamarck) (see Wrigley & Davis 1937, Curry 1958*a*, 1958*b*, 1962 MS.). The upper division has generally been regarded as Auversian (= Ledian = Lower Bartonian), owing to the occurrence in it of *Nummulites variolarius* (Lamarck), though there is other faunal evidence of its possibly closer affinity to the underlying Lutetian Stage (Curry 1962 MS.).

The Upper Bracklesham Beds, Fisher's division A or the *N. variolarius* zone, has

four principal fossil beds (a–d, Fisher 1862 : 67), of which the lower three (b–d) are represented in the exposure in Bracklesham Bay (Fisher 1862 : 74 ; Curry 1958*a*). The Polyzoan collection on which the present work is based came from (c), the highest bed but one, known as the Hard Bed or Fisher Bed 21, after the numbering scheme in Fisher's detailed section. This bed consists of " hard calcareous sand, with comminuted shelly matter and numerous *Tellinae* and other fossils " (Fisher 1862 : 74) ; it is overlain by a softer, clayey sand (b), rich in micro-fossils, termed the Clibs, and is underlain by clays, the *Beloptera* Bed and the *Cypraea* Bed (d), in descending order. The Hard Bed and the *Beloptera* Bed together constitute the Medmery Bed and with the overlying Clibs aggregate some 10 feet thick at Bracklesham Bay (Curry 1958*b* : 34). This group of beds occurs about half way up the Upper Bracklesham sequence and is of similar stratigraphical position to the *Tellina* and *N. variolarius* Beds of Whitecliff Bay, Isle of Wight (Curry 1958*b* : 34).

In contrast to the Polyzoa of the Lower Bracklesham Beds, which are predominantly encrusting forms (membraniporiform) adherent to the exteriors, and especially the interiors, of large molluscan shells, such as *Venericor*, *Clavilithes*, and *Sycostoma* (Davis 1934 : 205), the Cheilostomata of the Upper Bracklesham Beds include only a minority of encrusting types. Erect, arborescent (eschariform) and hollow, globular or discoidal (orbituliporiform ; see Morphology section below) zoaria occur in the greatest numbers ; erect, jointed (cellariiform) and membraniporiform zoaria are only slightly less frequent ; free, discoidal (lunulitiform) specimens are present in smaller numbers ; and fenestrate (reteporiform) zoaria are represented by only a few fragments (see Table I for the zoarial form and abundance of the species). The character of the Upper Bracklesham Cheilostomata, including both the excess of eschariform over membraniporiform zoaria and the relatively large diversity of species and genera, suggests accumulation in deeper, less turbulent water than that in which the Lower Bracklesham fauna lived (Davis 1934 : 205). The significant numbers of lunulitiform specimens attest to the granularity of the substrate, which was composed of shell fragments and Nummulitid and other larger foraminifers, as well as terrigenous detritus. Taken together, these data point to a biotope near the lower limit of effective wave action, perhaps at mid-sub-littoral depths, that is to say, 30–50 fathoms. The large cellariiform component could represent an epi-planktonic fauna essentially independent of bottom conditions. The growth requirements of the orbituliporiform species, making up so large a proportion of the Upper Bracklesham fauna, are, unfortunately, unknown ; however, Lagaaij (1963 : 203–207) has presented convincing arguments that *Fedora nodosa* Silén, a Recent species with somewhat similar growth form, is attached, at least initially, to small lumps of mud on the substrate in deep water (see Morphology section below).

The geographical connexions of the Upper Bracklesham Cheilostomata are more strongly Tethyan than those of any other division of the British Tertiary : 26 of the 38 species occur at least as far south-east as the Paris Basin (see Table II), whereas only 15 of the 29 Lower Bracklesham species and an even smaller proportion of the London Clay and Barton species do. Indeed, several of the Upper Bracklesham species, e.g. *Escharina procumbens* (Canu), *Hippopleurifera canui* nom. nov., and

TABLE I.—Zoarial form and abundance of Upper Bracklesham Cheilostomata

	O	E	C	L	M	R	T
1. *Orbitulipora petiolus* (Lonsdale)	149	—	—	—	—	—	149
2. *Schizostomella curryi* sp. nov.	—	109	—	—	—	—	109
3. *Vincularia monstruosa* (Canu)	—	—	94	—	—	—	94
4. *Lunulites transiens* Gregory	—	—	—	59	—	—	59
5. *Smittoidea variabilis* (Canu)	—	9	—	—	42	—	51
6. *Adeonellopsis punctata* (Canu)	—	45	—	—	—	—	45
7. *Entomaria dutempleana* (d'Orbigny)	—	43*	—	—	43*	—	43
8. *Setosellina gregoryi* sp. nov.	—	—	—	29*	29*	—	29
9. *Batopora glandiformis* (Gregory)	27	—	—	—	—	—	27
10. *Caberoides corniculatus* sp. nov.	—	—	27	—	—	—	27
11. *Escharoides aliferus* (Reuss)	—	24	—	—	—	—	24
12. *Teichopora clavata* Gregory	—	19	—	—	—	—	19
13. *Onychocella subpyriformis* (d'Archiac)	—	—	—	—	19	—	19
14. *Microporina magnipora* (Canu)	—	—	—	—	17	—	17
15. *Vincularia davisi* sp. nov.	—	—	15	—	—	—	15
16. *Celleporina thomasi* sp. nov.	—	—	—	—	12	—	12
17. *Tubucella mamillaris* (Milne Edwards)	—	9	—	—	—	—	9
18. *Sertella marginata* (Reuss)	—	—	—	—	—	9	9
19. *Schizostomella liancourti* (Canu)	—	7	—	—	—	—	7
20. *Nellia tenella* (Lamarck)	—	—	6	—	—	—	6
21. *Gaudryanella variabilis* Canu	—	6	—	—	—	—	6
22. *Labioporella? dartevellei* sp. nov.	—	6	—	—	—	—	6
23. *Cribrilaria parisiensis* (Canu)	—	—	—	—	5	—	5
24. *Membraniporella radiata* (Reuss)	—	4	—	—	—	—	4
25. *Escharella selseyensis* sp. nov.	—	—	—	—	4	—	4
26. *Ogivalina? dimorpha* (Canu)	—	3*	—	—	3*	—	3
27. *Kionidella hastingsae* sp. nov.	2	—	—	—	—	—	2
28. *Schizomavella trigonostoma* sp. nov.	—	2	—	—	—	—	2
29. *Poricellaria alata* d'Orbigny	—	—	2	—	—	—	2
30. *Escharina procumbens* (Canu)	—	2	—	—	—	—	2
31. *Hippoporina globulosa* (d'Orbigny)	—	—	—	—	2	—	2
32. *Adeonellopsis selseyensis* sp. nov.	—	1	—	—	—	—	1
33. *Dakaria beyrichi* (Stoliczka)	—	1	—	—	—	—	1
34. *Setosella fragilis* Canu	—	1	—	—	—	—	1
35. *Smittipora?* sp.	—	1	—	—	—	—	1
36. *Nellia ventricosa* (Canu)	—	—	1	—	—	—	1
37. *Exechonella* sp.	—	—	—	—	1	—	1
38. *Hippopleurifera canui* nom. nov.	—	—	—	—	1	—	1
TOTAL	178	246	145	59	103	9	815
		292*		88*	178*		

* Zoarial form uncertain. Abundance = number of zoaria and zoarial fragments. O = orbituliporiform; E = eschariform; C = cellariiform; L = lunulitiform; M = membraniporiform; R = reteporiform; T = total.

Nellia ventricosa (Canu), have not hitherto been reported north of the Aquitaine region of France. Most of the genera to which the Upper Bracklesham Cheilostomata belong, e.g. *Adeonellopsis* MacGillivray, *Dakaria* Jullien, *Escharina* Milne Edwards, *Escharoides* Milne Edwards, *Hippopleurifera* Canu & Bassler, *Sertella* Jullien, and

Smittoidea Osburn, to-day have rather wide latitudinal ranges but optima in the tropics or sub-tropics ; several, e.g. *Labioporella* Harmer, *Poricellaria* d'Orbigny, and *Setosellina* Calvet, are more distinctly tropical or sub-tropical ; and only a few, e.g. *Escharella* Gray and *Microporina* Levinsen, are more distinctly cool-water. The prevalence of warm-water genera seems, too, to be greater in the Upper Bracklesham fauna than in any other British Tertiary assemblage of Cheilostomata.

TABLE II.—Distribution of Upper Bracklesham Cheilostomata

	Pre-Ypres.	Ypres.	Lutet.	Auvers.	Bart.	Post-Bart.
1. *Ogivalina? dimorpha*	?Pal.	P	P, A	P	—	?Lud.
2. *Poricellaria alata*	?Pal.	—	P, A	E	—	Lud.
3. *Teichopora clavata*		P	P	E, ?B, P	E	
4. *Dakaria beyrichi*		P	P	B	—	Olig.
5. *Entomaria dutempleana*			B, P, A			
6. *Escharella selseyensis*			P			
7. *Gaudryanella variabilis*			P, A			
8. *Hippopleurifera canui*			A			
9. *Nellia ventricosa*			A			
10. *Schizostomella liancourti*			P			
11. *Setosella fragilis*			P			
12. *Escharina procumbens*			A	?A		
13. *Hippoporina globulosa*			P	B, P		
14. *Labioporella? dartevellei*			P	?B		
15. *Vincularia monstruosa*			P, A	?E		
16. *Adeonellopsis punctata*			P, A	—	—	?Lud.
17. *Escharoides aliferus*			P, A	—	—	Lud.
18. *Microporina magnipora*			A	—	—	?Lud.
19. *Onychocella subpyriformis*			E, P, A	B, P	?E, B	Lud.
20. *Smittoidea variabilis*			E, B, P	B	—	Lud.
21. *Membraniporella radiata*			P	B	—	Lud.
22. *Tubucella mamillaris*			B, P, A	B, P	—	Mio.
23. *Nellia tenella*			E, P, A	—	—	Rec.
24. *Lunulites transiens*				E	E	
25. *Setosellina gregoryi*				E, P	E, P	
26. *Orbitulipora petiolus*				E, B, P	B	Olig.
27. *Cribrilaria parisiensis*				B, P	B	Olig.
28. *Batopora glandiformis*					E	
29. *Sertella marginata*						Olig.
30. *Adeonellopsis selseyensis*						
31. *Caberoides corniculatus*						
32. *Celleporina thomasi*						
33. *Exechonella* sp.						
34. *Kionidella hastingsae*	KNOWN ONLY FROM THE UPPER BRACKLESHAM BEDS					
35. *Schizomavella trigonostoma*						
36. *Schizostomella curryi*						
37. *Smittipora?* sp.						
38. *Vincularia davisi*						

E = England ; B = Belgium ; P = Paris Basin ; A = Aquitaine region. Pal. = Palaeocene ; Lud. = Ludian ; Olig. = Oligocene ; Mio. = Miocene ; Rec. = Recent.

Stratigraphically, the Upper Bracklesham species compare most closely with the Lutetian fauna of the Continent : 25 of the 38 species have been recorded no lower than that stage, and six species no higher. Resemblance to the British Lutetian is much less : only three species, *Nellia tenella* (Lamarck), *Onychocella subpyriformis* (d'Archiac), and *Smittoidea variabilis* (Canu), are common to the Upper and Lower Brackleshams (cf. Davis 1934 : 208). Resemblance to Lower Eocene faunas—those of the London Clay and the Continental Ypresian—is lower still. Six species, *Batopora glandiformis* (Gregory), *Cribrilaria parisiensis* (Canu), *Lunulites transiens* Gregory, *Orbitulipora petiolus* (Lonsdale), *Sertella marginata* (Reuss), and *Setosellina gregoryi* sp. nov., are restricted to Auversian and higher units. A total of nine species is so far known only from the Upper Bracklesham Beds.

Despite their considerable resemblance to the French Lutetian fauna, the Upper Bracklesham Cheilostomata seem more likely to represent a late migrant, relict fauna related by descent to the strongly Tethys-influenced Parisian Middle Eocene fauna. Not only are six of the Upper Bracklesham species Auversian and younger guides as mentioned above, but also several of them are direct descendants of Continental Lutetian species : *Lunulites transiens* from *L. urceolata* Lamarck, *Caberoides corniculatus* from *C. canaliculatus* Canu, and *Kionidella hastingsae* from *K. obliqueseriata* Koschinsky. The origins of the Upper Bracklesham Cheilostomata have been traced as far as Senegal where Gorodiski & Balavoine (1962) encountered four of the species—*Nellia tenella*, *N. ventricosa*, *Labioporella? dartevellei* and *Ogivalina? dimorpha*—in rocks of Palaeocene to Lutetian age. The character of the Upper Bracklesham fauna thus seems to have an important bearing on the palaeogeographical relations between the London–Hampshire Basins and the Tethyan and boreal regions.

Davis & Elliott (1957) adduced evidence that the London and Hampshire Basins were on the south-west margin of an extensive north-west European sea in Ypresian times and that, as the sea transgressed over Belgium and into England from the north-east, it brought a boreal marine fauna into juxtaposition with a tropical terrestrial flora. As a result, both the shoal-water, sandy London Clay (in places with pebble beds) of the Hampshire Basin and the deeper-water London Clay of the London Basin contain a mixture of drifted tropical plant remains with molluscan shells belonging to such boreal genera as *Cyprina*, *Astarte*, *Pholadomya* and *Aporrhais* (Davis & Elliott 1957). At the close of London Clay deposition, the sea regressed eastwards spreading the " Lower Bagshot Sands " across the Hampshire Basin (Davis & Elliott 1957, Curry 1962 MS.).

The next transgressive phase, which began in the Cuisian and probably continued through the Lutetian and Auversian, resulted in prevalence of marine conditions in the Hampshire Basin where the Bracklesham Beds were deposited while the London Basin received sediments (the Bagshot Beds) which are at least in part deltaic (Curry 1962 MS.). The extreme western part of the Hampshire Basin, in the area around Bournemouth, retained non-marine conditions until Bartonian times. These relationships suggest that, whereas the London Clay transgression was essentially an extension of the North Sea, the Bracklesham Beds transgression was mainly,

if not entirely, a Tethyan invasion through the Channel. This interpretation seems not out of harmony with the distribution of marine Lutetian, Auversian, and Bartonian deposits in western Europe (see Denizot 1957 : pls. 4, 5). Shoal-water conditions in the Hampshire Basin during the deposition of the Lower Bracklesham Beds may well have prevented the greater number of Tethyan Cheilostomata coming until Auversian times. The Polyzoa from a mid-Channel Tertiary outlier probably of Cuisian or Lutetian age (Curry 1962 : 194) include genera—*Poricellaria*, *Vincularia*, *Lunulites*—of a facies more " Upper Bracklesham " than " Lower Bracklesham " and could thus represent the vanguard of the Selsey fauna.

III. PRESERVATION OF MATERIAL AND TECHNIQUE OF STUDY

The Upper Bracklesham Polyzoa from Selsey are in general very well preserved. Fine tuberculation, striation, and crenulation of the surfaces of many structures have been retained in extraordinary detail (see *Lunulites transiens*, Text-fig. 7 ; *Onychocella subpyriformis*, Text-fig. 10 ; *Entomaria dutempleana*, Text-figs. 25–27 ; and *Schizostomella curryi*, Text-figs. 67–70). Avicularian cross-bars are usually intact, but oral spines have invariably been broken (e.g. in *Hippopleurifera canui*, Text-fig. 39).

The effect of mechanical abrasion before interment is evident in species such as *Smittipora*? sp. (Text-fig. 12) and *Exechonella* sp. (Text-fig. 38) as well as in a few specimens of species in which the preservation is otherwise good (e.g. *Microporina magnipora*, Text-figs. 13, 14 ; and *Gaudryanella variabilis*, Text-figs. 23, 24).

Orifices, opesiae, avicularia, ovicells, and frontal pores are free of matrix in nearly all specimens studied.

Owing to its good preservation and to the very slight adherence of matrix to it, the material required no special preparation beyond the washing it had received before it was presented to the Museum.[1] During the course of their investigation, surface structures such as pits, pores, and striations were put into higher relief by staining the specimens with ordinary, water-soluble, green food-colour. So treated, many otherwise obscure structures became observable under 90 × magnification with a stereo-microscope in reflected light.

All the specimens were mounted on glass- or celluloid-covered, cardboard, microscope slides with gum-tragacanth.

Illustrations were prepared with a camera-lucida attachment on the stereomicroscope at 90 × magnification. Measurements were made on the specimens, rather than on the drawings (see Morphology section below for dimensions measured).

IV. REPOSITORIES FOR MATERIAL

British Museum (Natural History)

All the specimens in the Curry Collection have been retained in the Department of Palaeontology, where each has been given a number bearing the prefix " D ". The holotypes of new species and all the specimens figured in this work, whether they are primary types or not, have been drawn from the Curry Collection.

[1] Because the Tertiary formations exposed on the foreshore at Selsey are saturated with salt water, material collected from them requires several thorough rinses in fresh water to prevent deterioration of the fossils (Curry 1958*a*).

Geology Museum, Louisiana State University

Where possible, non-figured paratypes of the new species have been obtained from the additional Upper Bracklesham material given to me by Mr. Curry and have been deposited in the Geology Museum, Louisiana State University. These specimens, assigned numbers prefixed " L.S.U.", have been included in the abundance data shown in Table I.

V. MORPHOLOGY OF UPPER BRACKLESHAM CHEILOSTOMATA

Zoarial Characters

Growth habits of Cheilostomata have been analysed in detail by Stach (1936, 1937). To Stach's basic zoarial categories, Brown (1952 : 19, 32–35) added a number of forms which are fundamentally variations on the major growth themes. The main outlines of the Stach–Brown classification are followed here with few modifications.

Membraniporiform, lunulitiform, cellariiform, eschariform, and *reteporiform* patterns, for the most part, are recognizable in the Upper Bracklesham species. Owing to the fragmentary condition of most of the specimens, however, it is not always possible to distinguish between : (1) membraniporiform zoaria which have become detached from their substrate and eschariform zoaria which are unilaminar (either originally or by separation of bilaminar zoaria along discrete basal walls), or (2) cellariiform zoaria which have lost their articulating ends and eschariform zoaria with cylindrical (" vinculariiform ") branches. Some species, e.g. *Smittoidea variabilis,* include two growth forms, even in the same zoarium ; attendant variations in shape, size, and, to some extent, structure of zooecia can be a source of confusion in species determination (Text-figs. 42–46). There is also in some species gradation between zoarial forms resulting from small differences in substratal or other factors in the micro-habitat ; in *Setosellina gregoryi,* for example, the zoarium is alternatively membraniporiform or lunulitiform depending upon whether it started on a large or a small piece of shell or other detritus. In most of the species, however, the zoarial form is not so variable.

The *celleporiform* habit, essentially a variation of the membraniporiform one, seems not to be developed in Upper Bracklesham Cheilostomata with the possible exception of *Hippoporina globulosa* of which there are only two small fragments in the Curry Collection.

It is not possible in the Upper Bracklesham species to discriminate *vincullariiform*[1] and *adeoniform* zoaria from eschariform ones. In *Tubucella mamillaris,* for example, the zoarium begins from an encrusting base as a cylindrical (" vincullariiform ") stem, which, as it rises, soon gives way to lobate, flabellate (adeoniform) fronds, which, in turn, finally become broad and compressed (eschariform) branches (Text-fig. 62). Many of the Upper Bracklesham species, e.g. *Adeonellopsis punctata, Schizostomella curryi,* and *Smittoidea variabilis,* have this robust, dominating growth pattern, here characterized as eschariform.

[1] The term is an unfortunate one, as the genus *Vincularia* invariably displays the cellariiform habit.

Three species, *Orbitulipora petiolus*, *Batopora glandiformis*, and *Kionidella hastingsae*, assume a colonial growth form different from any heretofore characterized by the terms listed above and for which the name *orbituliporiform* is here proposed. The zoarium in all three species has a distinctive axial hollow round which the erect, prismatic zooecia are grouped in one or more layers. Unlike the similar hollow in *Conescharellina* d'Orbigny, that of the three species mentioned is devoid of tubules presumably derived from heterozooecia (see Silén 1947 : 33). In *Kionidella* the hollow extends nearly the full length of the unilaminar zoarium, its blind (proximal) end formed by the basal wall of the ancestrula and its open (distal) end formed by the basal walls of the most distal circlet of zooecia (Koschinsky 1885 : pl. 7, figs. 5–10). In *Batopora* the hollow runs only part way up the axis of the multilaminar zoarium whose ancestrular region is apparently obscured by superposed zooecia ; the distal end of the hollow is the basal pore surrounded by superposed zooecia (Waters 1919 : 84, pl. 6, figs. 4, 6, 10). In *Orbitulipora* the hollow is restricted to the basal peduncle of the zoarium, round the upper end of which the zoarium expands in a compressed bilaminar frond (Text-fig. 80 ; Canu & Bassler 1931 : pl. 3, figs. 1–22). According to Canu & Bassler (1931 : 17), the ancestrula lies at the upper end of the peduncular tube. The frond of *Orbitulipora* may be either flabellate, with all growth distal from the smaller zooecia, or circular, with growth radial from the smaller zooecia which thus become central. *Orbitulipora* and *Batopora* have the distal ends of the zooecia oriented towards the proximal end of the zoarium as in *Conescharellina*, whereas *Kionidella* has the distal ends of the zooecia directed distally as in typical Cheilostomata.

The mode of growth and the conditions for life of these and other orbituliporiform genera have not been established. Canu (1931 : 144–147) and Canu & Bassler (1931 : 19–21) supposed *Orbitulipora* to be free-swimming, the basal peduncle somehow lending locomotive force by a hydraulic process (presumably like that in the Cephalopoda?). Silén (1947 : 9) stated, concerning a somewhat similar mode of life in *Conescharellina* conjectured by Canu & Bassler (1929*b* : 482, 498), " It must be emphasized that this represents entirely an assumption by these authors and that nobody has ever observed such a phenomenon. Nevertheless the mentioned authors describe the movements of these zoaria in very vivid terms as if they had actually witnessed them." *Conescharellina* either rests upon its flat base on the substrate (and is, thus, lunulitiform) or, more probably, is suspended by chitinous tubes from floating objects (Silén 1947 : 13). On the other hand, the orbituliporiform zoaria of *Kionidella*, *Batopora*, and *Orbitulipora* and the similar ones of *Fedora nodosa* Silén and *F. edwardsi* Jullien (Silén 1947 : 53–55), with their unfilled axial cavities could result from " colonial growth taking place on and around small lumps of hardened mud, which would explain the irregular shape of the cavity " (Lagaaij 1963 : 203, 204). The chitinous tubes which frequently occupy the axial hollows of *Fedora nodosa*, supposed by Silén (1947 : 13) to be connexions between the globular zoaria of that species (which Silén argued were the internodes of a cellariiform zoarium), have proved to be the perisarcs of an associated Hydroid (Lagaaij 1963 : 204–206).

Zooecial Characters

The Upper Bracklesham Cheilostomata occupy such a broad band on the taxonomic spectrum—only four genera, *Nellia*, *Vincularia*, *Schizostomella*, and *Adeonellopsis*, are represented by more than one species, and no genus by more than two—that their zooecial morphology is extremely diverse. Thus, it is not possible to make generalizations about zooecial characters which would apply to the whole assemblage, and the remarks that follow are intended only as amplifications of certain points in the more exhaustive treatments of zooecial morphology contained in the works of Harmer (1926, 1957), Brown (1952), Larwood (1962) and others.

Zooecial walls. Basal, lateral, distal, and proximal walls, communication pores, and pore chambers are visible in some of the Upper Bracklesham specimens and are described where observed.

Walls associated with the frontal surface—including sub-frontal cryptocysts and frontal gymnocysts in the Anasca, super-frontal shields in the Acanthostega, and frontal walls in the Ascophora—are of first order significance in the classification of Cheilostomata and are described in as much detail in this work as the material permits. Descriptive terminology (e.g. perforate, marginally areolate) is preferred to a genetical one (e.g. tremocyst, pleurocyst).

Oral structure. In fossil Cheilostomata the structure of the primary orifice is discernible only in the Acanthostega and Ascophora; in the Anasca the orifice is lost during decomposition of the membranous frontal wall, though its form is indicated approximately by the size and shape of the opesia in species having an extensive cryptocyst, especially those belonging to the Microporidae, Poricellariidae, and related families. In the Ascophora the form of the primary orifice, which may be difficult to observe because of the development round it of a peristome with a secondary orifice usually more variable in form, is of paramount importance in classification at the generic level. In the Acanthostega " the shape of the primary orifice is not usually of diagnostic value " (Larwood 1962 : 35). In the present work, oral structure is described by referring to components (e.g. sinus, condyles) rather than to shape designations (e.g. hippoporine, cribriline) which are subject to personal interpretation.

Avicularia and vibracula. A variety of these structures is present in the Upper Bracklesham species : adventitious and vicarious avicularia and interzooecial vibracula (see Larwood 1962 : 41, for definitions of these terms). Vicarious avicularia are certainly more common than adventitious ones in the Anasca and vice versa in the Acanthostega and Ascophora, but exceptions to the general rule occur among the Poricellariidae and Farciminariidae in the Anasca and among the Adeonidae in the Ascophora. The vibraculum-bearing species are Anascans which belong to closely related families, Selenariidae and Lunulitidae.

In most of the Upper Bracklesham species, the avicularia or vibracula, whether adventitious, interzooecial, or vicarious, are well differentiated in form and structure from the normal zooecia. The avicularia often have pointed rostra and pivotal condyles or cross-bars. As noted by Larwood (1962 : 41) the absence of pointed

rostra or pivotal structures in fossils may be due to wear ; thus it is necessary to examine many specimens before it can be concluded that a species is characterized by avicularia with rounded rostra or without cross-bars. Most of the Upper Bracklesham material is so well preserved, however, that details of avicularian structure can be ascertained from even a few zooecia (see, e.g. *Hippopleurifera canui*, Text-fig. 39 ; *Escharina procumbens*, Text-figs. 56, 57). In some major taxa, e.g. the Ascophoran family Adeonidae, avicularia are regularly without condyles or cross-bar, but Brown's (1952 : 191) suggestion that adventitious avicularia in the Anasca are always without such structures is incorrect (see Harmer 1926 : pl. 14, figs. 18–20, *Nellia tenella* ; pl. 23, figs. 6–8, *Poricellaria ratoniensis*).

In four species of Upper Bracklesham Cheilostomata, belonging to widely separated families, vicarious avicularia[2] are only feebly differentiated from the normal zooecia. The differentiation is least in *Labioporella*? *dartevellei* (Text-figs. 21, 22) where it consists in slight enlargement of the avicularian (?) zooecia. In the two species of *Vincularia*, *V. monstruosa* (Text-figs. 30, 31) and *V. davisi* (Text-figs. 33, 34), the avicularian (?) zooecia have undergone curvature on their proximo-distal axis in addition to slight enlargement. The avicularian zooecia of *Schizostomella curryi* (Text-figs. 68, 70) are enlarged in the oral region in just the same way as the avicularia (= B-zooecia) are in *Steganoporella* (see Harmer 1926 : 268).

Ovicells and gonoecia. The systematic importance of the ovicell, one of the basic tenets upon which Canu & Bassler (1917, 1920, 1927, 1929*b*) established their classification of the Cheilostomata, has been seriously questioned by Silén (1944), Brown (1952), Lagaaij (1952) and Larwood (1962). The separation of five morphological types—hyperstomial, entozooecial, peristomial, vestibular, and entotoichal (Brown 1952 : 36, 37)—is still a useful descriptive device in spite of the large amount of mutual inter-gradation.

Hyperstomial ovicells are the most common type in the Upper Bracklesham Cheilostomata : 14 of the 38 species display them. Entozooecial ovicells occur in three species, and peristomial ovicells in one. None displays vestibular or entotoichal ovicells, though Canu (1925 : 47) described the ovicell of *Entomaria dutempleana* as entotoichal evidently through mis-interpretation (see Systematics section below and Text-fig. 27).

Five species, all belonging to the family Adeonidae, possess specially modified zooecia (gonoecia = gonozooecia of Brown 1952 : 37, not Cheetham 1962) instead of ovicelled zooecia. The gonoecia show a progressive series of modifications in the Upper Bracklesham Adeonidae from the feebly differentiated dimorphs of the ordinary zooecia of *Teichopora clavata* (Text-figs. 65, 66), through the distally swollen, orally modified gonoecia of *Schizostomella curryi* (Text-figs. 67–69) and *Adeonellopsis selseyensis* (Text-fig. 73), to the generally swollen, orally and frontally modified gonoecia of *Adeonellopsis punctata* (Text-figs. 74, 75).

The remaining 15 species of Upper Bracklesham Cheilostomata apparently lack specially modified fertile zooecia of any sort.

[2] It is possible that these features are other forms of zooecial dimorphs in the four species concerned.

Measurements

Certain linear dimensions are usually measured in descriptive work on Cheilostomata (Canu & Bassler 1920, 1923; Osburn 1950, 1952; Brown 1952; Lagaaij 1952; Larwood 1962; Cheetham 1962, 1963*b*). For the Upper Bracklesham species the following are recorded:

Lz = zooecial length, the maximum distance between the zooecial proximal and distal margins projected to the proximo-distal axis of the frontal surface.

lz = zooecial width, the maximum distance between the zooecial lateral margins measured perpendicular to the proximo-distal axis of the frontal surface.

ho = oral or opesial length, measured in the same direction as the proximo-distal axis of the zooecial frontal surface and always in the plane of the orifice or opesia even where that plane is not parallel to the frontal surface.

(For sinuate orifices, oral length includes the sinus.)

lo = oral or opesial width, measured perpendicular to oral or opesial length.

(Oral dimensions are taken at the primary orifice where possible; where measurements of secondary orifice are substituted, a notation to that effect is given in the Measurements section of the species description.)

Lov = ovicell length, the maximum distance between the proximal and distal margins of the ovicell projected to the proximo-distal axis of its frontal surface.

(Ovicell length is determined only for hyperstomial ovicells, owing to the lack of definite margins in entozooecial and peristomial ones. The full length, width, and oral dimensions of gonoecia are recorded for species in which those structures supplant ovicelled zooecia.)

Lav or *Lv* = avicularian or vibracular length, the maximum distance between rostrum and opposite margin measured in the plane of the avicularian or vibracular upper surface.

(Width and oral dimensions are recorded for vicarious avicularia only.)

Zoarial dimensions are recorded for reteporiform and orbituliporiform species only.

The arithmetic mean and standard deviation of each linear dimension of each species are calculated by the standard formulae, and the number of specimens measured and the observed range of the dimension are recorded. For brevity, the following scheme of presentation is used throughout the Systematics part of this paper:

Lz	(10)	0·500	(0·0500) mm.	0·45–0·55 mm.
Character symbol	(Number of specimens)	Mean	(Standard deviation)	Observed range

All dimensions are in decimal fractions of a millimeter, the observed range expressed to the nearest 0·01 mm., and the mean and standard deviation carried, respectively, one and two places farther. Measurements were taken with a 15× micrometer ocular in an American Optical stereo-microscope fitted with 6× objective, and each

observation was recorded to the nearest whole micrometer division. Means, standard deviations, and observed ranges are calculated in micrometer units and then converted to millimeters by the factor 0·00855 mm. per micrometer unit.

Taxonomic significance of measurements. Assessment of the value of quantitative characters as a discriminatory tool in Cheilostome taxonomy has barely been started by studies of variation in a few species (e.g. the works of Illies 1953 and David & Mongereau 1961). The pessimistic feelings of most workers are probably typified by the remarks of Brown (1952 : 33, 34) that " no great importance is attached to the value of . . . measurements as they are found to vary widely even in the same colony," or that " they are seldom to be used as the basis for differentiating species in the absence of other differences of a more positive character " (see also Larwood 1962 : 45, 46). Lack of evaluation has not kept some authors from founding species chiefly, or even solely (see Canu & Bassler 1919 : 89, *Steganoporella parvicella*), on dimensional criteria. Examples of quantitative discrimination which has subsequently proved erroneous are provided by some of Lang's Cretaceous Cribrimorphs (revised by Larwood 1962) and some of Canu & Bassler's Tertiary species of *Steganoporella* (revised by Cheetham 1963*b*).

Knowledge of the magnitude of variability is crucial to the assessment of any dimensional character as a taxonomic criterion. Yet most authors who have described Cheilostomata have failed to include any meaningful measure of variability in their specific characterizations, despite the fact that they have given some form of measurement. They have generally followed Canu in giving either a single, " typical " value, perhaps obtained as the arithmetic mean of an unstated number of observations, or a range of values obtained as the extremes of an again unstated number of observations. Either alternative gives almost no information about the dispersion of the character in the sample at hand or in the population from which it was drawn (Simpson, Roe & Lewontin 1960 : 78–82).

Variance and standard deviation are certainly the most widely used measures of variability in statistical work. From the standard deviation may be calculated, not only the standard error from which confidence limits for the population mean may be obtained, but also, a measure of relative variability, Pearson's coefficient of variation, from the formula

$$V = \frac{100s}{\bar{x}}.$$

By use of V's so obtained, it is possible to compare variation of a character in different samples of the same species or in different species (Simpson, Roe & Lewontin 1960 : 90).

For the Upper Bracklesham species, it is necessary to correct the V's, because of small sample size, by Haldane's method (Simpson, Roe & Lewontin 1960 : 101, 102) :

$$V_c = \frac{V(4N + 1)}{4N}.$$

The values of V_c for the Upper Bracklesham species are presented in Table III.

TABLE III.—Corrected coefficients of variability of linear dimensions of Upper Bracklesham Cheilostomata

	Lz	lz	ho	lo	Lov	Lav or Lv
1. *Ogivalina? dimorpha*	13·9	23·2	17·0	16·5	—	—
2. *Setosellina gregoryi*	9·5	12·7	10·2	12·5	—	10·4
3. *Lunulites transiens*	8·2	4·5	13·4	9·8	—	18·9
4. *Onychocella subpyriformis*	15·8	10·5	10·2	11·4	—	6·3
5. *Smittipora?* sp.	11·7	6·4	11·9	14·9	—	—
6. *Microporina magnipora*	6·2	12·8	4·4	5·8	—	—
7. *Setosella fragilis*	2·9	7·9	7·4	11·1	—	—
8. *Poricellaria alata*	6·4	9·4	13·2	0·0	—	18·2
9. *Labioporella? dartevellei*	5·6	11·8	9·8	22·2	—	—
10. *Gaudryanella varibilis*	9·7	13·7	10·0	14·8	—	—
11. *Entomaria dutempleana*	12·9	10·0	23·0	9·9	—	22·2
12. *Nellia tenella*	4·2	10·8	10·5	12·2	—	23·0
13. *Nellia ventricosa*	4·1	17·8	5·2	25·1	—	10·2
14. *Vincularia monstruosa*	8·2	10·9	9·8	6·7	—	[a] 23·4 / 6·8
15. *Vincularia davisi*	8·9	6·3	3·3	10·7	—	6·8
16. *Cribrilaria parisiensis*	6·0	13·2	10·8	7·9	5·2	12·8
17. *Membraniporella radiata*	4·3	15·0	10·0	13·2	6·3	5·2
18. *Exechonella* sp.	4·0	6·8	12·3	10·4	—	—
19. *Hippopleurifera canui*	3·3	3·4	6·1	12·7	—	—
20. *Escharoides aliferus*	12·0	12·1	14·3	4·5	10·6	22·3
21. *Smittoidea variabilis*	[b] 15·2 / 17·0	12·5 / 20·8	10·4	9·1	7·8 / 8·7	17·8
22. *Escharella selseyensis*	15·9	14·8	13·6	4·9	6·2	—
23. *Sertella marginata*	6·6	6·7	18·4	13·6	9·2	[c] 21·6 / 17·3 — 8·3 / 17·7
24. *Dakaria beyrichi*	6·8	14·4	19·6	7·4	—	—
25. *Schizomavella trigonostoma*	12·8	26·8	13·0	5·2	—	15·6
26. *Escharina procumbens*	10·8	23·2	8·5	9·3	0·0	12·0
27. *Hippoporina globulosa*	17·0	13·4	7·3	4·6	3·6	3·0
28. *Caberoides corniculatus*	6·6	10·9	10·4	7·6	1·5	7·0
29. *Tubucella mamillaris*	9·9	13·2	15·1	18·5	—	—
30. *Teichopora clavata*	3·3	5·5	9·1	12·7	5·2	[d] 12·9 / 13·1
31. *Schizostomella curryi*	9·1	3·1	11·5	12·5	3·6	[d] 22·4 / 16·1
32. *Schizostomella liancourti*	12·1	15·9	19·8	12·1	—	17·6
33. *Adeonellopsis selseyensis*	9·9	6·7	8·8	6·0	3·3	9·0
34. *Adeonellopsis punctata*	13·9	9·6	12·7	7·9	7·1	18·2
35. *Celleporina thomasi*	13·2	10·4	13·9	5·4	6·6	8·8
36. *Kionidella hastingsae*	20·8	6·5	6·5	8·9	10·8	14·8
37. *Orbitulipora petiolus*	11·3	13·4	20·1	9·5	11·6	—
38. *Batopora glandiformis*	18·4	14·3	12·5	19·9	11·4	0·0

[a] Vicarious and adventitious avicularia. [b] Zooecia on uni- and bilaminar fragments. [c] Polymorphic avicularia. [d] Dimorphic avicularia. Lz, lz, ho and lo exclude modified zooecia.

The significance of coefficients of variation can be judged by comparing *V*'s for many species, a procedure which Simpson, Roe & Lewontin (1960 : 90) deemed

" generally valid if the variates are analogous and belong to the same category—for instance, if they are all linear dimensions of anatomical elements ".[3] For mammals, linear dimensions yield " hundreds of V's, . . . the great majority " of which " lie between 4 and 10, and 5 and 6 are good average values " (Simpson, Roe & Lewontin 1960 : 91). By this standard, the Upper Bracklesham Polyzoa are extraordinarily variable. David & Mongereau (1961), in their study of *Cellaria fistulosa* auctt. *non* Linné, obtained variances and means from which V's of 6·9 for zooecial length and 9·0 for zooecial width may be calculated. These are lower than for most of the Upper Bracklesham species, though comparable to the ones for species having cellariiform zoaria.

In order to broaden the comparison of variability of characters, it is possible to include in this analysis two American Early Tertiary assemblages of Cheilostomata (Cheetham 1962, 1963*b*) for which $\bar{x}$, s, and N of standard dimensions have been recorded. V's are calculated and corrected by the same formulae used for the Upper Bracklesham species. Then, for each linear dimension, the number of species in the combined fauna having V_c less than 10·0 is entered in Table IV. These species numbers are expressed as percentages of the total number of species showing the character, and for each percentage approximate 95% confidence limits are calculated by the formula

$$p_{0\cdot 95} = p \pm 2\sqrt{\frac{p(1-p)}{N}}$$

(Sylvester-Bradley 1958 : 222).

The value 10·0 was chosen as the limit between high V's and low ones, not just because Simpson, Roe & Lewontin considered values of 4–10 to be usual, but also because variability amounting to no more than 10% of the mean indicates a relatively small overlap between populations even where the difference between their means is fairly small. For example, if normal distribution of the variate is postulated for each of two populations A and B, 90% of A will be distinct from 90% of B even where the difference between their means ($|\bar{x}_A - \bar{x}_B|$) amounts to no more than 0·128 ($\bar{x}_A + \bar{x}_B$), provided that their V's are 10 or less and that their variances are approximately equal.[4] Canu & Bassler (1920 : 262, 263), as mentioned above, established two species of *Steganoporella* on a difference in mean zooecial width of this magnitude ($|\bar{x}_A - \bar{x}_B| = 0{\cdot}12$ mm. ; $0{\cdot}128\ (\bar{x}_A + \bar{x}_B) = 0{\cdot}077$ mm.), but, unfortunately, the variation in that character was subsequently shown (Cheetham 1963*b* : 54–56) to be much too great, at $V = 18{\cdot}2$, for specific separation. On the other hand, the difference in mean zooecial lengths of two of the Upper Bracklesham species, *Vincularia monstruosa* and *V. davisi*, at 0·162 mm.,[5] is greater than 0·128 ($\bar{x}_A + \bar{x}_B$) = 0·133 mm.,

[3] Reyment (1963 : 684) regarded as valid only comparisons of the same character.

[4] Ninety per cent. joint non-overlap is regarded as the minimum requirement for separate taxonomic status by some systematists (e.g. Mayr, Linsley & Usinger 1953 : 145). However, as Sylvester-Bradley (1958 : 225–227) has pointed out, overlap in several uncorrelated characters taken simultaneously may be less than 10% even where any single one shows overlap of more than 10%.

The expression $0{\cdot}128(\bar{x}_A+\bar{x}_B)$ may be derived from Mayr, Linsley & Usinger's (1953 : 146) coefficient of difference, by substituting $S_A = 0{\cdot}10\bar{x}_A$ and $S_B = 0{\cdot}10\bar{x}_B$.

[5] Even if the nearer limits of their 95% confidence intervals are used, the difference indicates 87·5% non-overlap.

and both V's are less than 10 ; thus the two species are approximately 90% distinct in this dimension (and, in addition, show other differences " of a more positive character ").

TABLE IV.—Relative variability of linear dimensions of Cheilostomata (Based upon data from the Upper Bracklesham species and from Cheetham 1962, 1963*b*)

	No. Spp.	No. Spp. $V_e < 10{\cdot}0$	%	Conf. limits
A. Relatively constant characters:				
1. Length of vicarious avicularium	12	10	83·3	61·7 – 104·9
2. Width of primary orifice	38	31	81·6	68·0 – 95·2
3. Length of ovicell or gonoecium	33	24	72·7	57·0 – 88·4
B. Relatively variable characters :				
1. Length of zooecium	89	48	53·9	43·3 – 64·5
2. Width of zooecium	88	45	51·1	40·3 – 61·9
3. Length of primary orifice	38	18	47·4	31·2 – 63·6
4. Length of opesia not separate from opesiules	27	12	44·4	25·3 – 63·5
5. Length of avicularium or vibraculum regardless of position	43	16	37·2	22·5 – 51·9
6. Width of opesia not separate from opesiules	27	9	33·3	15·2 – 51·4
7. Length of adventitious avicularium	30	6	20·0	5·4 – 34·6
C. Characters for which evidence is insufficient to judge variability :				
1. Length of opesia separate from opesiules	8	5	72·7	28·3 – 96·7
2. Width of opesia separate from opesiules	8	4	50·0	14·6 – 85·4
3. Length of interzooecial vibraculum	4	2	50·0	0·0 – 100·0
4. Width of secondary orifice	12	5	41·7	13·2 – 70·2
5. Length of secondary orifice	15	6	40·0	14·7 – 65·3

It must be emphasized that, in comparisons of the sort exemplified here, " the mean is a necessary statistic but it cannot be used on its own to test assumptions of difference in dimensions. For this one requires a statistic which is able to express the spread of the data " (Reyment 1963 : 684). Therefore, it is of the utmost importance that a measure of variability be attached to all data which are presented

in a taxonomic context. The coefficient of variation, though useful in preliminary assessment of single variates of the type illustrated here, is not employed in multivariate analysis.

This first evaluation of linear dimensions in Eocene Cheilostomata, summarized in Table IV, has identified three characters—length of vicarious avicularium, width of primary orifice, and length of ovicell or gonoecium—as relatively less variable than most. As one or more of these are measurable in most species of Cheilostomata, they are potentially useful in discrimination of species and sub-species. Even the comparatively more variable characters, especially zooecial length and width, are sufficiently constant in some species for use as a taxonomic criterion as shown above. Only one dimension, length of adventitious avicularium, seems so variable as to be taxonomically almost useless. How much of the variability in the latter character is due to differential breakage of these vulnerable structures must remain for the present one of the imponderables.

VI. CLASSIFICATION AND GENERAL ARRANGEMENT

The Upper Bracklesham Cheilostomata include representatives of all three sub-orders: Anasca, 15 species; Acanthostega (= Cribrimorpha; see Cheetham 1963*b* : 60), 2 species; and Ascophora, 21 species.

The supra-generic classification of the order is seriously in need of overhaul, but such a project is not within the compass of the present work. Thus no categories between sub-order and family are employed here, and some of the families, e.g. Hincksinidae, are accepted only provisionally. Most of the families used here have been accepted by Harmer (1926, 1934, 1957), but a few, e.g. Selenariidae and Farciminariidae in the Anasca and Ditaxiporinidae in the Ascophora, are not found in his works. The family Labioporellidae Harmer is not deemed sufficiently distinct from the Steganoporellidae for recognition here. I do not follow Harmer (1957 : 824) in suppressing the well-known name Tubucellariidae in favour of the obscure Margarettidae based upon the senior synonym for the type genus.

The scheme of presentation of the systematic sections of this work is similar to those used by Brown (1952) and Larwood (1962).

Families and taxa of higher categories are not defined here as definitions are available in recent literature.

Genera. Only those genera for which new information, including revision or clarification, is presented are diagnosed in this work. For each genus diagnosed, the synonymy (including only the original reference and references to name changes), the type species, the diagnosis, and remarks on nomenclature or taxonomy are given in that order. In the diagnoses, characters are described in approximate order of taxonomic importance: (1) frontal wall and associated structures, (2) oral structures, (3) heterozooecia, (4) ovicells or gonoecia, (5) interzooecial communication, (6) zooecial shape and arrangement, and (7) zoarial form.

Species. Every species studied, including the two left *nomina aperta*, is described. For each, a detailed synonymy is given first, and a list of the material studied, type and non-type, figured and non-figured specimens, next. The species diagnosis and

then its description, based on all material available, follow the list of specimens ; some features, e.g. ovicells or avicularia, lacking in the material at hand but described in the literature, are included in the species descriptions by reference to the pertinent literature. Measurements (see Morphology section above for scheme of presentation) and remarks on nomenclature and taxonomy follow the species description. Finally, under distribution is summarized the known stratigraphical and geographical extent of the species as compiled from the literature.

VII. SYSTEMATIC DESCRIPTIONS

Phylum POLYZOA

Class *ECTOPROCTA*

Subclass *GYMNOLAEMATA*

Order CHEILOSTOMATA

Suborder ANASCA

Family **HINCKSINIDAE** Canu & Bassler

Genus ***OGIVALINA*** Canu & Bassler

1917 *Ogivalina* Canu & Bassler : 16.

TYPE SPECIES (by original designation). *Ogivalina eximipora* Canu & Bassler 1917 : 17, pl. 2, fig. 1. Eocene (Jacksonian) ; Castle Hayne Marl, Wilmington, North Carolina, U.S.A.

DIAGNOSIS. Frontal wall membranous, gymnocyst greatly reduced or lacking. Cryptocyst well developed, especially proximally, coarsely granular. Opesia large, oval to sub-circular, without distinct opesiular indentations. Avicularia interzooecial or lacking, not initiating new zooecial rows, with pointed rostra, lacking cryptocyst or pivotal structures. Ovicell entozooecial, inconspicuous. Interzooecial communication by pores without chambers.

Ogivalina? dimorpha (Canu)

(Text-figs. 1–3)

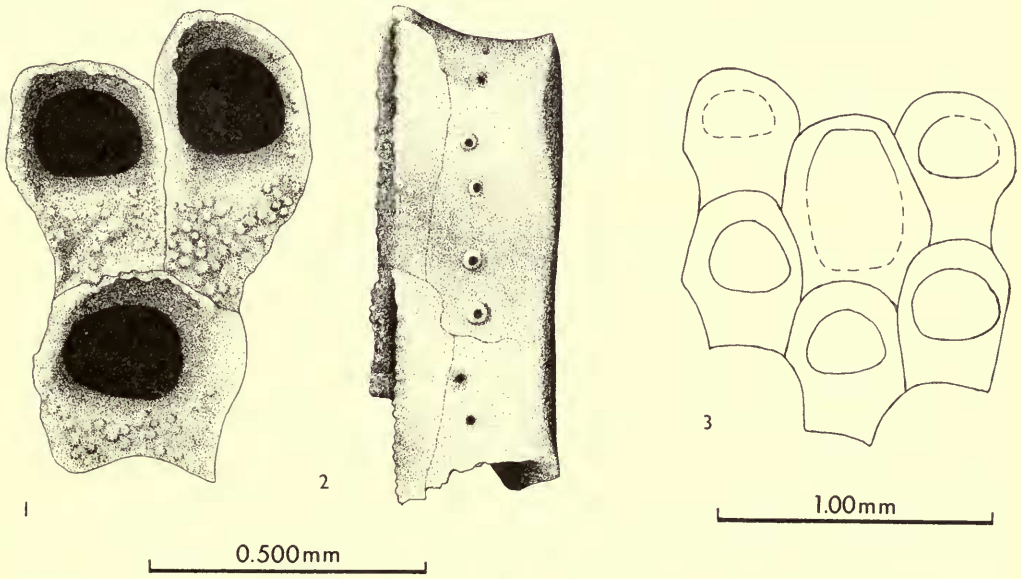
1907*b* *Onychocella dimorpha* Canu : 79, pl. 11, figs. 1–3.
1926 *Onychocella dimorpha* Canu ; Canu : 749, pl. 27, fig. 6.
1933 *Onychocella dimorpha* Canu ; Dartevelle : 106.
1935 *Rectonychocella dimorpha* (Canu) Dartevelle : 112.
1936 *Onychocella dimorpha* Canu ; Dartevelle : 29.
1946 *Stamenocella? dimorpha* (Canu) Buge : 431.
1949 *Onychocella dimorpha* Canu ; Balavoine : 773.
1960 *Stamenocella dimorpha* (Canu) ; Balavoine : 246.
?1962 *Stamenocella dimorpha* (Canu) ; Gorodiski & Balavoine : 5.
?1963 *Vibracella trapezoidea* (Reuss) ; Malecki : 109, pl. 10, fig. 9.

FIGURED SPECIMENS. D.48341 (Text-fig. 1), D.48342 (Text-fig. 2), D.48343 (Text-fig. 3).

DIAGNOSIS. *Ogivalina* (?) with dimorphic zooecia, the ordinary ones with very extensive cryptocyst and transversely elliptical opesia, the " membraniporoid " ones without cryptocyst ; avicularia large, pointed, sometimes initiating zooecial rows.

DESCRIPTION. *Zoarium* encrusting or erect, uni- or bilaminar, the zooecia arranged in easily separable, longitudinal rows ; in bilaminar fragments, the two laminae are easily separable.

Zooecia separated by faint grooves between beaded mural rims, dimorphic : (1) *Ordinary zooecia* claviform, broadly rounded distally, straight sided proximally ; width variable from about half length to just over length ; cryptocyst well developed, imperforate, finely and evenly tuberculate except where worn, relatively flat and little depressed below mural rim, descending slightly towards opesia ; opesia subcircular to elliptical, its major axis transverse, completely rimmed by a smooth collar forming a narrow shelf distally and a steeply descending " oral lamina " (see Canu 1907*b* : 79) proximally. (2) " *Membraniporoid* " *zooecia* rhomboidal, straight sided distally as well as proximally ; width regularly two-thirds length (see Canu 1907*b* : 79) ; cryptocyst lacking ; opesia elliptical, its major axis longitudinal, without distal shelf or proximal " oral lamina ".



FIGS. 1–3. Fig. 1. *Ogivalina*? *dimorpha* (Canu). D.48341. Three ordinary zooecia. Fig. 2. *Ogivalina*? *dimorpha* (Canu). D.48342. Two ordinary zooecia in lateral aspect. Fig. 3. *Ogivalina*? *dimorpha* (Canu). D.48343. Outline drawing of five ordinary zooecia and one " membraniporoid " zooecium.

Interzooecial communication by a single row of about 12 simple pores near middle of lateral and distal walls.

Avicularia lacking in material at hand.

Ovicell unknown.

Measurements :

Ordinary zooecia

Lz (10) 0·486 (0·0659) mm., 0·37–0·56 mm.
lz (10) 0·380 (0·0860) mm., 0·26–0·49 mm.
ho (10) 0·216 (0·0358) mm., 0·16–0·26 mm.
lo (10) 0·276 (0·0432) mm., 0·20–0·32 mm.

" Membraniporoid " zooecia

Lz (1) 0·62 mm. ho (1) 0·56 mm.
lz (1) 0·44 mm. lo (1) 0·37 mm.

Remarks. The generic position of this distinctive species remains doubtful. It resembles the American Eocene *O. eximipora* Canu & Bassler (1917 : 17, pl. 2, fig. 1 ; 1920 : 118, pl. 23, figs. 6, 7) in the following characters : (1) shape, size, and mode of communication of zooecia ; (2) extent and ornamentation of the cryptocyst ; (3) general shape of opesia and presence of a descending " oral lamina " on its proximal margin ; (4) form and position of avicularia (*fide* Canu 1907*b* : pl. 11, figs. 1–3). The Upper Bracklesham specimens lack avicularia but resemble the French specimens illustrated by Canu in other respects.

Distribution. ?Palaeocene ; Senegal. Eocene (Ypresian, Lutetian, Auversian); France. ?Eocene (Ludian) ; Poland.

Family **SELENARIIDAE** Busk

Genus ***SETOSELLINA*** Calvet

1906 *Setosellina* Calvet : 157.
1917 *Vibracellina* Canu & Bassler : 14.

Type species (by monotypy). *Setosellina roulei* Calvet 1906 : 157. Recent ; Cape Verde Islands.

Diagnosis. Frontal membranous, gymnocyst reduced. Cryptocyst very narrow, not widened proximally. Opesia oval to sub-pyriform, wider proximally, without differentiated opesiular indentations. Vibracula interzooecial, one placed at distal end of each zooecium ; vibracular opesia reniform. Ovicell lacking. Zoarium encrusting, in later stages of growth usually becoming free and discoidal ; zooecial rows originate by spiral growth from ancestrula.

Setosellina gregoryi[6] sp. nov.

(Text-figs. 4–6)

1893 *Biselenaria offa* Gregory : 235 [*partim*—pl. 30, fig. 5 ; *non* pl. 30, figs. 4, 4*a* (=*Orbitulipora petiolus*)].
1907*b* *Biselenaria offa* Gregory ; Canu : 85, pl. 12, figs. 1–3.
1926 *Vibracellina offa* (Gregory) Canu : 747.
1929 *Biselenaria offa* Gregory ; Burton : 348.
1933 *Vibracellina offa* (Gregory) ; Dartevelle : 106, 113.
1936 *Vibracellina offa* (Gregory) ; Dartevelle : 29.
1946 *Biselenaria offa* Gregory ; Buge : 430.

Holotype. D.48344 (Text-fig. 6).

Paratypes. D.48346 (Text-fig. 4), D.48345 (Text-fig. 5), D.48347–371 (26 specimens), and L.S.U. 8032.

Diagnosis. *Setosellina* with zoarium free and discoidal in later stages, zooecia arranged in anti-clockwise spirals round small ancestrula ; basal side of zoarium flat or slightly concave, formed of smooth, irregularly radiating sectors ; peripheral ring of large or small vibracula on basal surface.

Description. *Zoarium* unilaminar, encrusting shell fragments or Nummulitids in early stages, becoming free and discoidal in later stages. Zooecia arranged in two repeatedly bifurcating, anti-clockwise, spirally coiled lines, each one emanating from a vibraculum on the lateral margin of the central ancestrula. Basal surface flat or slightly concave, with solid, smooth, irregularly radiating sectors projecting from marginal zooecia back to ancestrular region.

Ancestrula slightly more than half as long as mature zooecia, otherwise of the same form. First two post-ancestrular zooecia slightly larger. Succeeding zooecia all of full size. Ancestrula, and less frequently the two small zooecia, partly closed by a calcareous lamina with a central pore.

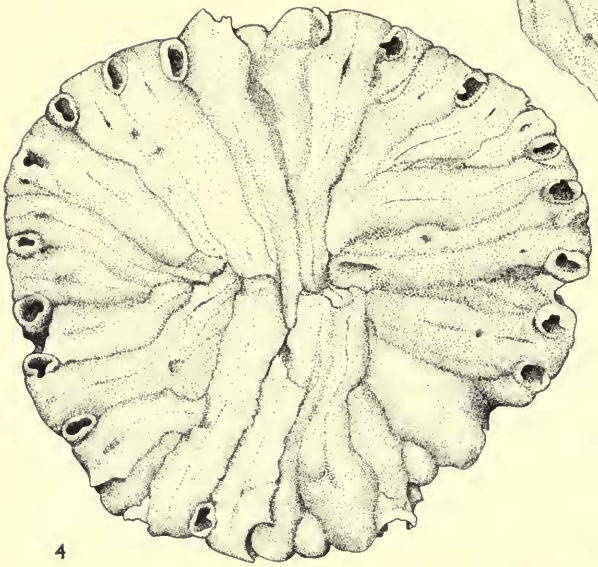
Zooecia irregularly oval, separated by deep grooves. Length slightly greater than width. Gymnocyst smooth, convex, narrow, extending entirely round zooecium but developed best proximally and laterally. Mural rim sharp, smooth, not raised. Cryptocyst very narrow, forming a horse-shoe laterally and proximally, descending steeply all round the opesia ; surface finely granular and radially striated. Interzooecial communication by a few simple pores in distal and lateral walls.

Opesia irregularly oval to elliptical, without differentiated opesiular indentations.

Vibracula interzooecial, usually smaller than zooecia, one placed at distal end of each zooecium, except ancestrula which has two lateral vibracula. Vibracular opesia reniform, its main axis an extension of that of its proximal zooecium ; vibracular condyle on right larger than that on left. Vibracula on periphery of basal surface of same form as those on frontal side of zoarium but occasionally greatly enlarged.

Ovicell lacking.

[6] After the late J. W. Gregory.



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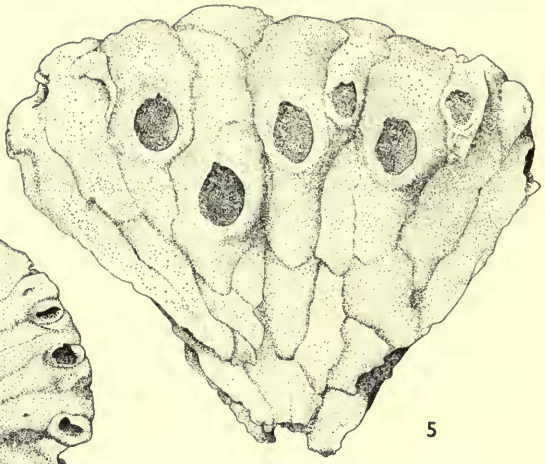

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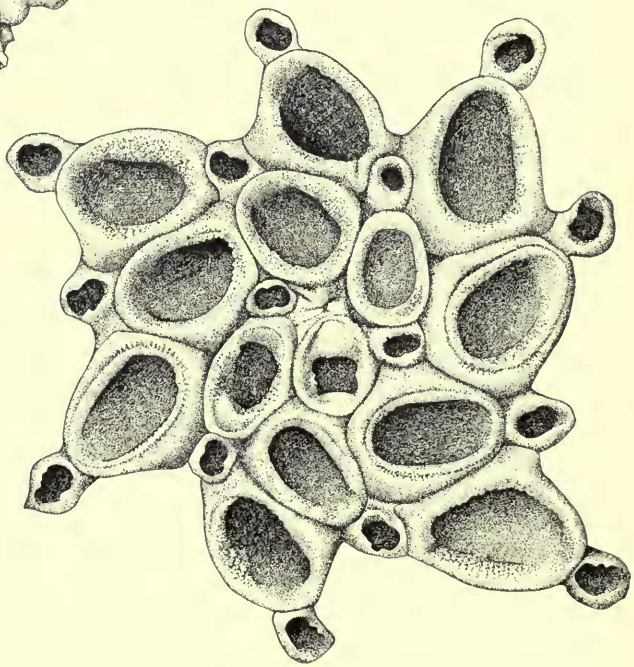

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MEASUREMENTS :

Ancestrula

Lz (4) 0·180 (0·0121) mm., 0·17–0·20 mm.
lz (4) 0·143 (0·0117) mm., 0·13–0·15 mm.
ho (4) 0·132 (0·0049) mm., 0·13–0·14 mm.
lo (4) 0·081 (0·0110) mm., 0·07–0·09 mm.
Lv (4) 0·086 (0·0000) mm., 0·09 mm.

Mature zooecia

Lz (10) 0·302 (0·0280) mm., 0·26–0·36 mm.
lz (10) 0·250 (0·0310) mm., 0·21–0·30 mm.
ho (10) 0·211 (0·0210) mm., 0·19–0·26 mm.
lo (10) 0·129 (0·0158) mm., 0·10–0·16 mm.
Lv (10) 0·120 (0·0121) mm., 0·10–0·14 mm.

REMARKS. Gregory (1893 : 235) described *Biselenaria offa* from the Barton Beds, Barton, Hants., on the basis of three specimens on slide 49759, Edwards Collection, illustrated on his plate 30 as " Fig. 4. Zoarium of type specimen : upper surface. Fig. 4*a*. Part of another specimen : under surface. Fig. 5. Upper surface of another zoarium." The specimens illustrated on his figs. 4 and 4*a* are conspecific with *Cellepora petiolus* Lonsdale, the type species of *Orbitulipora* (see description of that species below). The third specimen is conspecific with the material referred to by Canu, Burton, Dartevelle and Buge as " *Biselenaria offa* Gregory ". Unfortunately, as Gregory clearly designated as holotype one of the specimens of *Orbitulipora petiolus*, there is no alternative to giving this species a new name.

S. gregoryi is a guide species to Upper Eocene (Auversian and Bartonian) strata on both sides of the Channel. It has its nearest counterpart in the Recent Mediterranean species *S. capriensis* (Waters) in which the zoarium is more conical with a more concave base, the zooecia are larger and arranged in clockwise spirals, and the peripheral vibracula are placed on the edge of the zoarium rather than on the basal surface. *S. goesi* (Silén), a Recent Caribbean and Gulf of Mexico species, encrusts larger grains than the other two species and thus never becomes fully lunulitiform. Lagaaij (1963 : 172) reported both clockwise and anti-clockwise spirals in *S. goesi*. The coincidence of the smaller vibracular condyle and the direction of coiling of the zooecial rows noted by Lagaaij in *S. goesi* is also distinguishable in *S. gregoryi*.

DISTRIBUTION. Eocene (Auversian, Bartonian) ; England, France.

FIGS. 4–6. Fig. 4. *Setosellina gregoryi* sp. nov. D.48346. Paratype. Basal view of a small, nearly complete zoarium. Fig. 5. *Setosellina gregoryi* sp. nov. D.48345. Paratype. Basal view of a larger, fragmentary zoarium. Fig. 6. *Setosellina gregoryi* sp. nov. D.48344. Holotype. Ancestrular region showing zooecia and vibracula.

Family **LUNULITIDAE** Lagaaij

Genus ***LUNULITES*** Lamarck

Lunulites transiens Gregory

(Text-figs. 7–9)

1850 *Lunulites urceolata* Lamarck ; Lonsdale : 159, pl. 1, fig. 8.
1878 *Lunulites urceolata* Lamarck ; Lonsdale : 201, pl. 1, fig. 8.
1893 *Lunulites transiens* Gregory : 233, pl. 29, figs. 13, 14 ; pl. 30, fig. 1.
1933 *Lunulites transiens* Gregory ; Dartevelle : 106, 113.

Holotype. 49724, Edwards Collection. Barton Clay ; Barton, Hants. Figured by Gregory (1893, pl. 29, fig. 14).

Figured specimens. D.48372 (Text-fig. 7), D.48373 (Text-fig. 8), D.48374 (Text-fig. 9).

Additional material. Fifty-six specimens, D.48375–D.48430.

Diagnosis. *Lunulites* with discoidal, slightly concavo-convex zoarium, basal surface divided into irregular, finely perforate, radial sectors ; new zooecial rows originating from vibracular rows ; mural rims of adjacent zooecia confluent, forming thick, high transverse ridge between zooecia of same row ; cryptocyst very narrow, shelf-like.

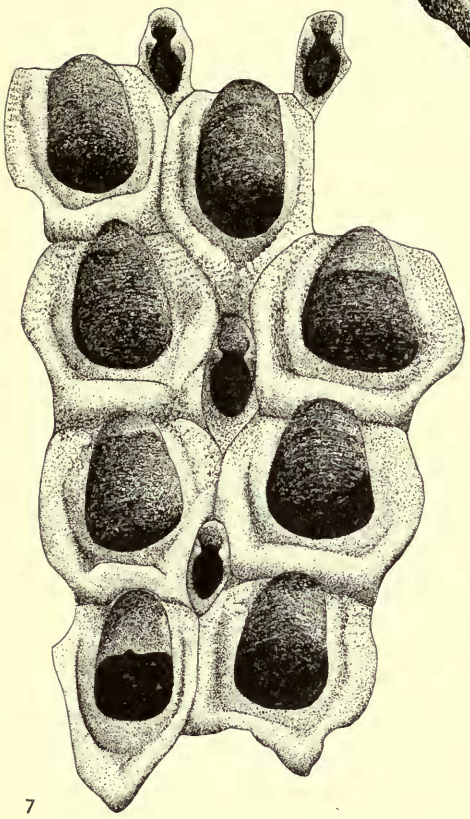
Description. *Zoarium* free in adult stages, discoidal, probably circular in outline, the upper surface moderately convex, the basal side slightly concave. Ancestrula encrusts *Nummulites* or small shell fragment which usually shows at centre of basal surface. Zooecia arranged in radial lines emanating from central ancestrula or from central fragment of an older zoarium from which regeneration has occurred. Vibracula occur in similar radial lines alternating with zooecia, one at every zooecial corner, except at points of intercalation of new zooecial rows. New zooecial rows originate from vibracular rows, the first zooecium of the new row lacking vibracula at its proximo-lateral corners, but having a single one proximally. Basal surface of zoarium with irregular, radial, finely perforated sectors, increasing in number peripherally by intercalation, separated by deep furrows.

Zooecia rhomboidal, slightly longer than wide, their mural rims confluent. Mural rim granular, broad and low laterally, but rising rapidly proximally to form a wide, thick, transverse wall separating cryptocyst of distal zooecium from opesia of proximal one. Cryptocyst a flat, imperforate, finely granular, very narrow shelf on proximal and lateral margins of opesia.

Opesia oval, more broadly rounded proximally than distally, without differentiated indentations.

Communication between zooecia by a single, large pore placed in middle of distal wall and a similar pore in each lateral wall.

Vibracula interzooecial, slightly shorter and much narrower than zooecia, rhombic, symmetrical, those of a series increasing in size distally. Vibracular opesia sym-



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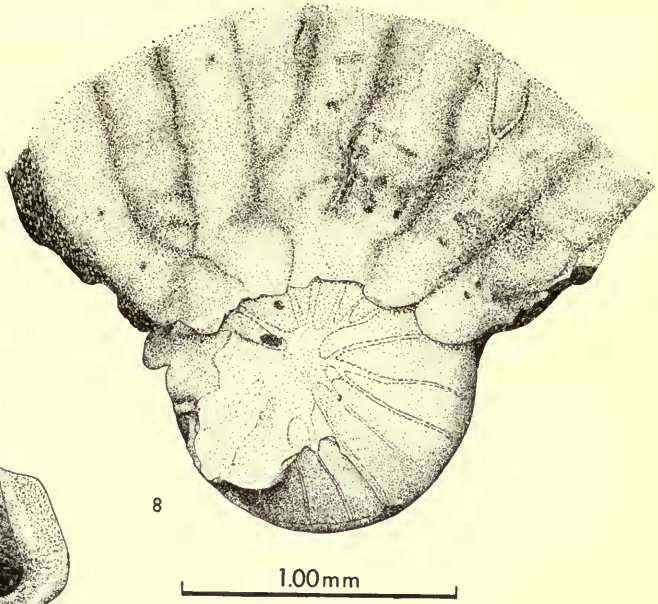

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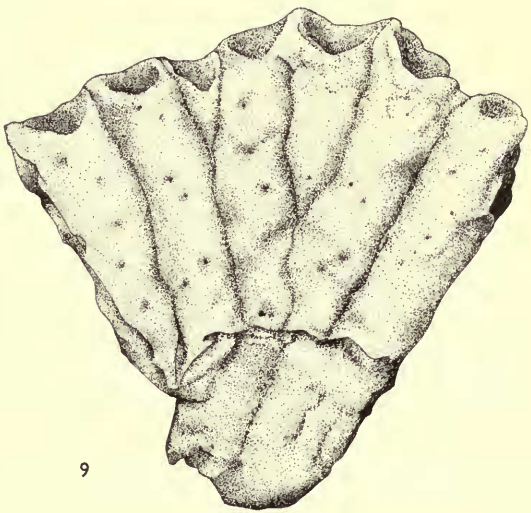

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FIGS. 7–9. Fig. 7. *Lunulites transiens* Gregory. D.48372. Eight zooecia and four vibracula. Zooecium at upper right is primoserial, budded from a vibraculum. Fig. 8. *Lunulites transiens* Gregory. D.48373. Basal aspect of a fragmentary zoarium emanating from a small Nummulitid test. Fig. 9. *Lunulites transiens* Gregory. D.48374. Basal aspect of a fragmentary zoarium regenerated from an older zoarial fragment.

metrical, oval, divided by a pair of stout condyles into a small distal portion and a much larger proximal one.

Ovicell lacking.

Measurements :

Ordinary zooecia

Lz (5) 0·340 (0·0266) mm., 0·30–0·37 mm.
lz (5) 0·290 (0·0127) mm., 0·27–0·31 mm.
ho (5) 0·238 (0·0305) mm., 0·20–0·27 mm.
lo (5) 0·166 (0·0155) mm., 0·14–0·18 mm.

Primoserial zooecia

Lz (5) 0·398 (0·0239) mm., 0·36–0·42 mm.
lz (5) 0·260 (0·0076) mm., 0·26–0·27 mm.
ho (5) 0·231 (0·0326) mm., 0·20–0·24 mm.
lo (5) 0·137 (0·0086) mm., 0·13–0·14 mm.

Vibracula

Lv (5) 0·197 (0·0354) mm., 0·17–0·23 mm.
lv (5) 0·077 (0·0166) mm., 0·06–0·10 mm.

Vibracula proximal to primoserial zooecia

Lv (5) 0·327 (0·0245) mm., 0·30–0·36 mm.
lv (5) 0·162 (0·0270) mm., 0·14–0·20 mm.

Remarks. Canu (1907*b* : 83), in re-describing and illustrating *L. urceolata* Lamarck, has given several criteria for the separation of the French Lutetian species from *L. transiens*. Of these, the shape of the zoarium and the development of the cryptocyst seem to be the most readily applicable.

The pattern of increase in number of zooecial rows exhibited by *L. transiens*, although distinctive, is by no means unique as Gregory (1893 : 233) implied. Among the American Tertiary species of *Lunulites*, *L. distans* Lonsdale and *L. fenestrata* (de Gregorio) show the same pattern. In *L. jacksonensis* (Canu & Bassler), *L. ligulata* (Canu & Bassler) and *L. tintinabula* (Canu & Bassler) increase is by bifurcation of zooecial rows ; in *L. bouei* Lea and *L. truncata* de Gregorio it is accomplished by bifurcation of vibracular rows with intercalation of zooecial rows between them. Among the European Tertiary species the *L. transiens* pattern seems to be much more widespread. Perhaps these patterns will make possible subgeneric partition of the very inclusive genus *Lunulites*.

Distribution. Eocene (Auversian, Bartonian) ; England.

Family **ONYCHOCELLIDAE** Jullien

Genus ***ONYCHOCELLA*** Jullien

Onychocella subpyriformis (d'Archiac)

(Text-figs. 10, 11)

1846 *Eschara subpyriformis* d'Archiac : 195, pl. 5, figs. 21, 21*a*.
?1851 *Semieschara parisiensis* d'Orbigny : 366.
1869*a* *Membranipora angulosa* (Reuss) ; Reuss : 253, pl. 29, figs. 9–11.
1891 *Onychocella angulosa* (Reuss) Waters : 9.
1907*b* *Onychocella angulosa* (Reuss) ; Canu : 21, pl. 11, fig. 11.
1910 *Onychocella angulosa* (Reuss) ; Canu : 840, 844.
1916 *Onychocella angulosa* (Reuss) ; Faura y Sans & Canu : 298.
1925 *Onychocella angulosa* var. *parisiensis* (d'Orbigny) ; Canu : 46.
1926 *Onychocella angulosa* var. *parisiensis* (d'Orbigny) ; Canu : 748, pl. 27, fig. 7.
?1929 *Onychocella* n. sp., Burton : 328.
1929*a* *Onychocella angulosa* (Reuss) ; Canu & Bassler : 24.
1930 *Onychocella parisiensis* (d'Orbigny) ; Canu & Bassler : 22.
1933 *Onychocella parisiensis* (d'Orbigny) ; Dartevelle : 64, 106, 113.
1934 *Onychocella parisiensis* (d'Orbigny) ; Davis : 220.
1935 *Onychocella parisiensis* (d'Orbigny) ; Dartevelle : 112.
1936 *Onychocella parisiensis* (d'Orbigny) ; Dartevelle : 26.
1946 *Onychocella angulosa* var. *parisiensis* (d'Orbigny) ; Buge : 430.
1949 *Onychocella angulosa* (Reuss) ; Balavoine : 773.
1951 *Onychocella angulosa* (Reuss) ; Kyri : 71.
1956 *Onychocella parisiensis* (d'Orbigny) ; Balavoine : 321.
1957 *Onychocella angulosa* var. *parisiensis* (d'Orbigny) ; Balavoine : 191.
1960 *Onychocella parisiensis* (d'Orbigny) ; Balavoine : 246.
?1962 *Onychocella angulosa* (Reuss) ; Ghiurca, table 1.
?1963 *Onychocella angulosa* (Reuss) ; Malecki : 104, pl. 9, fig. 14.
1963 *Onychocella angulosa* (Reuss) ; Braga : 23, pl. 2, fig. 5.

Figured specimens. D.48431 (Text-fig. 10), D.48432 (Text-fig. 11).

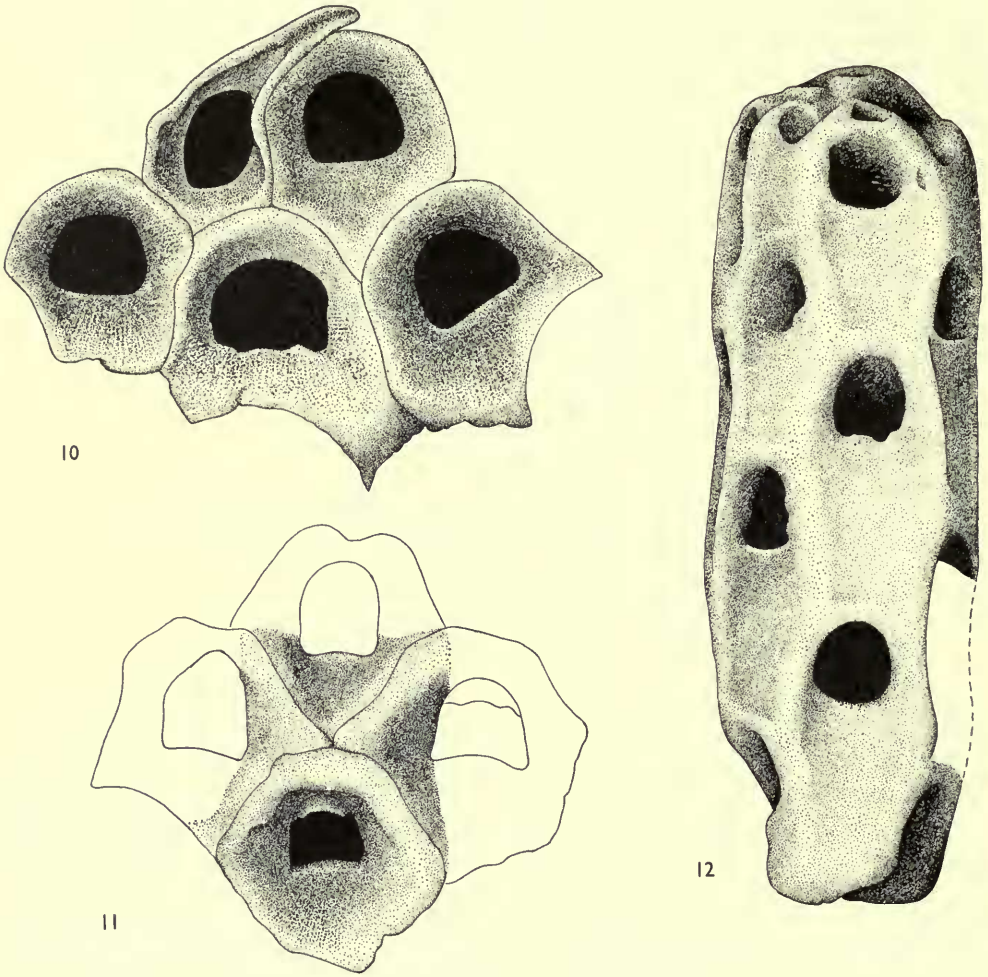
Additional material. Seventeen specimens, D.48433–D.48449.

Diagnosis. *Onychocella* with zooecial opesia semi-circular, oval, or sub-pyriform and sub-terminal on cryptocyst, in some zooecia with distinct distal shelf ; opesiular indentations not differentiated ; avicularian opesia more broadly rounded distally than proximally.

Description. *Zoarium* encrusting, but probably rising in unilaminar, erect, tubular fronds, the zooecia arranged in irregular, alternating rows. Additional rows originate from an avicularium inserted between rows of zooecia.

Zooecia hexagonal, pentagonal, or rhomboidal, separated by a faint groove at the crest of the confluent mural rims. Zooecial length and width subequal, both extremely variable. Mural rim thin, sharp, and finely granular in most zooecia, but thickened and raised in some ; gymnocyst lacking. Cryptocyst extensive, markedly concave, present all round the opesia, widest proximally. Surface of cryptocyst imperforate, finely granular, merging with mural rim.

Opesia sub-terminal on the cryptocyst, extremely variable in size, semi-circular, oval, or sub-pyriform, the distal margin evenly rounded, the proximal margin straight, slightly convex, or slightly concave ; distinct distal shelf present in opesiae of zooecia with thickened mural rims. Opesiular indentations not differentiated from opesia.



FIGS. 10–12. Fig. 10. *Onychocella subpyriformis* (d'Archiac). D.48431. Four zooecia and an onychocellarian avicularium. Fig. 11. *Onychocella subpyriformis* (d'Archiac). D.48432. Four zooecia partly shaded to show details of the raised and thickened mural rim and the distal opesial shelf of the zooecium at lower centre. Fig. 12. *Smittipora*? sp. D.48450. Fragment with worn and slightly broken zooecia.

Avicularia vicarious, longer but narrower than zooecia, with mural rim and cryptocyst identical with those of zooecia. Inwardly directed processes of mural rim separate elongate rostrum from short proximal part. Rostrum channelled, acutely pointed, directed sharply to either right or left, its axis diverging at angles of about 30° from main axis of avicularium. Avicularian opesia symmetrical, oval, more broadly rounded distally, sometimes pointed proximally, undivided by condyles or pivotal bar.

Ovicell lacking, but zooecia with nearly terminal opesiae may be fertile ones.

MEASUREMENTS :

Ordinary zooecia

Lz	(10) 0·362 (0·0557)	mm., 0·31–0·49 mm.
lz	(10) 0·353 (0·0361)	mm., 0·30–0·39 mm.
ho	(10) 0·153 (0·0153)	mm., 0·13–0·18 mm.
lo	(10) 0·174 (0·0194)	mm., 0·14–0·21 mm.

Zooecia with distal opesial shelf

ho	(5) 0·128 (0·0264)	mm., 0·10–0·17 mm.
lo	(5) 0·133 (0·0076)	mm., 0·13–0·14 mm.

Avicularia

Lav	(5) 0·506 (0·0305)	mm., 0·46–0·55 mm.
lav	(5) 0·258 (0·0159)	mm., 0·23–0·27 mm.
ho	(5) 0·171 (0·0121)	mm., 0·15–0·18 mm.
lo	(5) 0·118 (0·0113)	mm., 0·10–0·13 mm.

REMARKS. Canu (1910 : 844) recognized that d'Archiac's species is the same as the Eocene species identified by most authors with *O. angulosa* (Reuss), but, when he sorted the species out (1926 : 748), he used the unfortunate (and junior) name *Onychocella parisiensis* (d'Orbigny). The synonymy is further complicated by the existence of two Cretaceous species of *Onychocella*, *O. subpyriformis* (Hagenow) and *O. parisiensis* (d'Orbigny), whose names are homonyms of the Eocene species.

O. angulosa s.s., the Oligocene-Recent type species of *Onychocella*, is distinguished from *O. subpyriformis* by its sub-central opesia and its less angulated avicularian rostrum (see Reuss 1848 : pl. 11, fig. 10 ; Harmer 1926 : pl. 16, fig. 8).

DISTRIBUTION. Eocene (Lutetian, Auversian) ; France. Eocene (Auversian, Bartonian) ; Belgium, Spain. ?Eocene (Bartonian) ; England. Eocene (Ludian) ; Italy, Rumania, ?Poland.

Genus ***SMITTIPORA*** Jullien

Smittipora? sp.

(Text-fig. 12)

FIGURED SPECIMEN. D.48450 (Text-fig. 12).

Description. *Zoarium* erect, cylindrical, slender, composed of 6 longitudinal rows of zooecia alternating in position.

Zooecia separated by faint grooves at crest of confluent mural rims, rhomboidal to claviform ; length slightly less than twice width. Gymnocyst lacking. Mural rim worn, rather thick. Cryptocyst extends about two-thirds zooecial length from proximal margin ; surface slightly depressed, perceptibly concave, merging with mural rim peripherally, granular, imperforate.

Opesia terminal on cryptocyst, sub-circular, more broadly rounded proximally than distally, without differentiated indentations.

Heterozooecia, ovicells not present.

Measurements :

Lz	(5) 0·446 (0·0496)	mm., 0·38–0·50 mm.
lz	(5) 0·253 (0·0155)	mm., 0·23–0·27 mm.
ho	(5) 0·135 (0·0153)	mm., 0·11–0·14 mm.
lo	(5) 0·125 (0·0177)	mm., 0·10–0·14 mm.

Remarks. This species, represented solely by the fragment illustrated, resembles *Smittipora midwayanica* Canu & Bassler (1920 : 225, pl. 4, figs. 16–19) from the Palaeocene of Arkansas, U.S.A. It differs from the latter species in having fewer rows of larger zooecia with shorter opesiae. It also resembles *Glauconome prismatica* Hagenow and *G. canalifera* Hagenow, Cretaceous species often referred erroneously to *Vincularia* (see Berthelsen 1962 : 67–69). *Siphonella cylindrica* Hagenow is another Cretaceous form with similar zooecial and zoarial morphology but with a hollow zoarium (see Voigt 1951 : 61, 62). The generic assignment of these so-called vincularian forms can be resolved better by instituting a new genus for them than by distorting the Farciminariid genus *Vincularia* to accommodate them (see discussion of that genus below).

Family **MICROPORIDAE** Gray

Genus ***MICROPORINA*** Levinsen

1909 *Microporina* Levinsen : 162.

Type species (chosen by Bassler 1935). *Cellularia articulata* Fabricius 1824 : 27 (as *Salicornaria borealis* Busk 1855 : 254, pl. 1, figs. 1–3). Recent ; Greenland, 73° 20′ N., 57° 20′ W., 6–10 fms.

Diagnosis. Frontal wall membranous, without gymnocyst. Cryptocyst completely developed, shallow, flat, not greatly depressed in region of opesiules, finely and evenly perforate. Opesia approximately co-extensive with orifice, terminal, semi-circular to elliptical, with straight, slightly concave, or slightly convex proximal lip. Opesiules simple, small, circular or elliptical, inconspicuous, paired, one placed on each side of opesia and just proximal to it. Some of lateral cryptocystal pores probably serve as auxiliary opesiules in some species. Avicularia common or rare (or absent?), interzooecial, small, with pivotal bar and pointed rostrum, developed

between zooecia of the same longitudinal row. Zooecia variable in size and shape, even in a single colony. Zoarium encrusting, erect-unilaminar or erect-jointed.

Remarks. This genus differs from *Calpensia* in having avicularia, from *Micropora* in lacking ovicells, and from both in having simple, not tubular opesiules. Kluge (1962 : 322) has done much to clarify the characters of the genus and its type species.

Microporina magnipora (Canu)

(Text-figs. 13, 14)

1914*a* *Micropora magnipora* Canu : 299, pl. 4, figs. 1, 2.
?1963 *Steginoporella elegans* (Milne Edwards) ; Malecki : 111, pl. 11, fig. 6.

Figured specimens. D.48451 (Text-fig. 13), D.48452 (Text-fig. 14).

Additional material. Fifteen specimens, D. 48453–D.48467.

Diagnosis. Unilaminar, encrusting to erect *Microporina* with large, rhomboidal zooecia ; opesiules not much larger than frontal pores ; avicularia lacking (?).

Description. *Zoarium* unilaminar, encrusting or forming erect, flat or hollow-tubular masses, composed of zooecia arranged in regular, occasionally bifurcating, longitudinal rows, those in adjacent rows alternating in position.

Zooecia separated by a very faint groove, rhomboidal, but becoming distorted or abortive in some parts of zoarium. Length almost twice width. Gymnocyst lacking. Mural rim finely granular, rounded, narrow distally, widening slightly proximally, raised round distal margin of opesia to form a half-collar. Interzooecial communication by a few large pores in lower half of distal and lateral walls.

Cryptocyst complete, extending from proximal margin more than three-quarters of the zooecial length. Surface nearly flat, depressed well below level of mural rim, deepest at centre, evenly perforated by large, quincuncially arranged pores, of which the lateral ones probably served as auxiliary opesiules. Opesiules simple pores, occasionally with slightly raised margins, one placed in each of the two disto-lateral corners of the cryptocyst, just proximal to opesia.

Opesia semi-circular, terminal, approximately co-extensive with orifice. Distal margin evenly rounded. Proximal margin nearly straight, but usually broken.

Avicularia and *ovicells* not present.

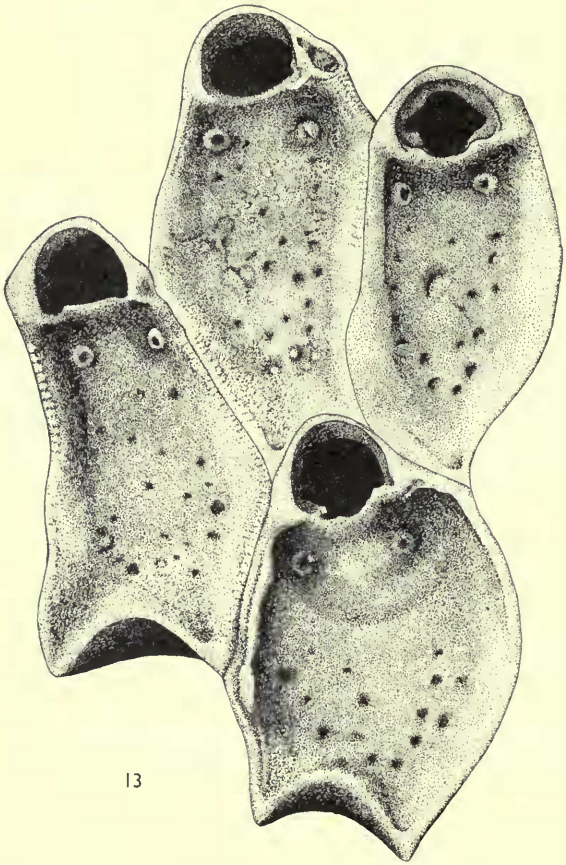
Measurements :

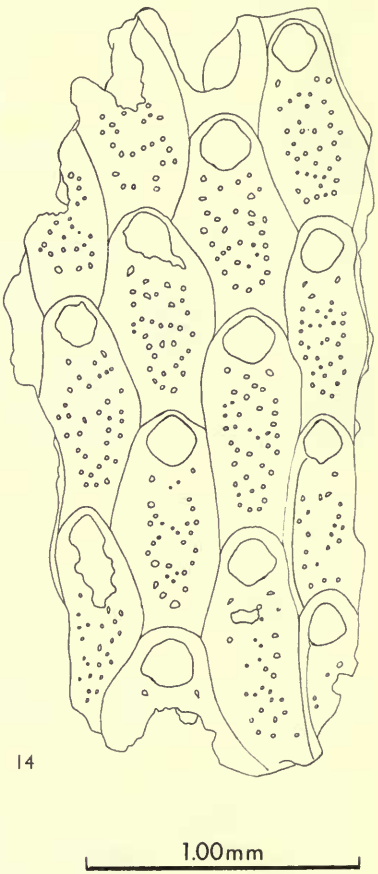
Lz	(10)	0·742 (0·0450) mm., 0·66–0·81 mm.
lz	(10)	0·398 (0·0497) mm., 0·34–0·50 mm.
ho	(6)	0·151 (0·0064) mm., 0·14–0·15 mm.
lo	(10)	0·180 (0·0102) mm., 0·17–0·20 mm.

Remarks. This species is very similar in both zooecial and zoarial characters to *Poropeltarion lebanonense* Cheetham (1963*b* : 50, pl. 1, figs. 5, 11) and *P. newelli*

Cheetham (1963*b* : 51, pl. 1, figs. 9, 10) from the Middle and Upper Eocene of Florida, U.S.A., but my suggestion (Cheetham 1963*b* : 50) that *M. magnipora* may belong to *Poropeltarion* has not been substantiated. The clearly differentiated opesiules of *M. magnipora* indicate that it should be assigned to *Microporina* despite the absence of avicularia. Dr. H. D. Thomas (personal communication, 1962) reports that a species of *Microporina* from the London Clay has avicularia only very occasionally. Whether *M. magnipora* proves to have avicularia or not, it forms a link with the slightly younger American *Poropeltarion*.

DISTRIBUTION. Eocene (Lutetian); France. ?Eocene (Ludian); Poland.





FIGS. 13–14. Fig. 13. *Microporina magnipora* (Canu). D.48451. Four zooecia from a slightly irregular part of a zoarium, probably near a point of branching. Fig. 14. *Microporina magnipora* (Canu). D.48452. Fragmentary zoarium showing more regularly arranged zooecia.

Genus *SETOSELLA* Hincks

1877 *Setosella* Hincks : 529.

Type species (by original designation). *Membranipora vulnerata* Busk 1860 : 124, pl. 25, fig. 3. Recent; British Isles.

Diagnosis. Frontal wall membranous, with reduced gymnocyst laterally and proximally. Cryptocyst completely developed, imperforate except for a pair of lateral, longitudinal, slit-like opesiules near lateral margins. Opesia small, semicircular, terminal, co-extensive with orifice. Vibracula (missing in some species?) small, interzooecial, one at the distal end of each zooecium, the vibracular opesia reniform. Ovicell lacking, but fertile zooecia with swollen distal wall exhibiting a small depressed area and usually with a widened opesia.

Remarks. Jullien (1882 : 524, pl. 17, fig. 66) was the first to describe and illustrate fertile zooecia in the type species of *Setosella*, but he interpreted them as having entotoichal (= " cassiform ") ovicells. This interpretation led Levinsen (1909 : 196) to establish a family, Setosellidae, to which later authors added *Entomaria* Duvergier (see discussion of the ovicell of that genus below) and other genera (see Bassler 1953 : 174). Material of *S. vulnerata* in the Department of Zoology, British Museum (Natural History), e.g. 99.7.1.1490, Busk Collection, shows the structure of the gonoecium clearly : the " ovicell " is simply a post-oral swelling in the distal wall not separated internally from the zooecium, and the " pore " is simply a frontal depression on the distal part of the gonoecium.

Absence of a distinct ovicell, as well as differences in zooecial structure, makes it necessary to remove *Setosella* from such genera as *Lagarozoum, Entomaria, Crateropora,* and *Aspidostoma,* for which the family name Aspidostomatidae Jullien is available (see Brown 1952 : 148–153). *Setosella* can be given temporary accommodation in the Microporidae.

Setosella fragilis Canu

(Text-figs. 15, 16)

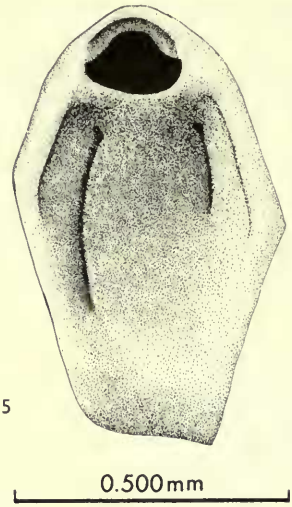
1907*b* *Setosella fragilis* Canu : 140, pl. 19, fig. 15.
1946 *Setosella fragilis* Canu; Buge : 433.

Figured specimen. D.48468 (Text-figs. 15, 16).

Diagnosis. Erect, cylindrical *Setosella* arising from encrusting base ; zooecia without gymnocyst ; vibracula lacking ; gonoecia unknown.

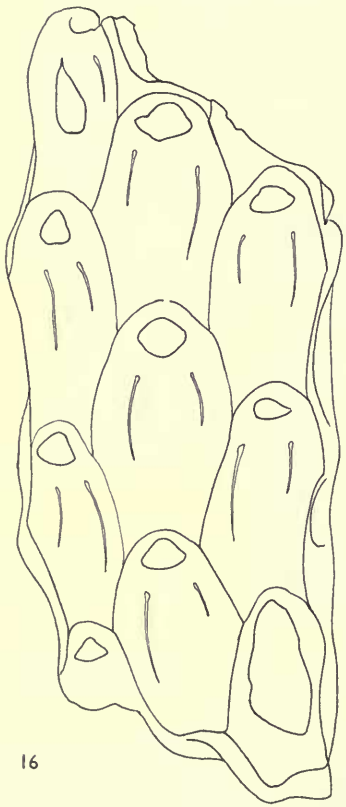
Description. *Zoarium* erect, cylindrical, presumably arising from an encrusting base, the zooecia arranged in 8 longitudinal rows, those in adjacent rows alternating in position.

Zooecia regularly rhomboidal, rounded distally, straight sided proximally, separated by a faint groove at the crest of the confluent mural rims. Length about one and a half times width. Gymnocyst lacking. Mural rim smooth, probably abraded in the specimen studied, narrow all round the zooecium, not raised distally.



15

0.500mm



16

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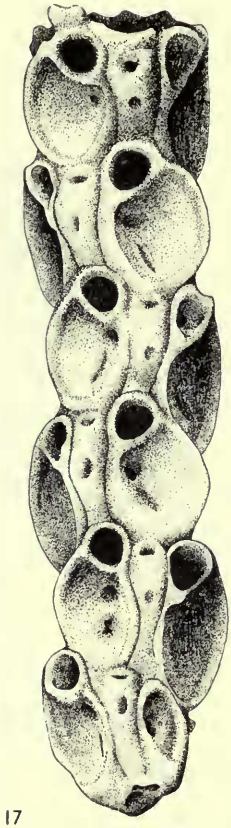


17

18

0.500mm

Cryptocyst completely developed, extending from proximal margin more than three-quarters of the zooecial length. Surface somewhat undulating, convex and little depressed in proximal third, concave and moderately depressed in middle third, rising markedly in distal third; imperforate and smooth. Opesiules slit-like, unequal, one paralleling each lateral margin, removed slightly from mural rim. Longer opesiule, either right or left, markedly arcuate, extending from near proximal lip of opesia almost the whole length of the cryptocyst. Shorter opesiule less arcuate, extending from near proximal lip of opesia about half the length of the cryptocyst.

Opesia semi-elliptical, terminal, approximately co-extensive with orifice. Distal margin evenly rounded. Proximal margin much more broadly rounded.

Heterozooecia and *gonoecia* not observed.

Measurements:

Lz (7) 0·757 (0·0209) mm., 0·70–0·81 mm.
lz (7) 0·486 (0·0340) mm., 0·44–0·54 mm.
ho (7) 0·134 (0·0095) mm., 0·13–0·15 mm.
lo (7) 0·184 (0·0197) mm., 0·15–0·20 mm.

Remarks. My earlier suggestion (Cheetham 1963*b*: 50) that this species might belong to *Poropeltarion* has proved erroneous. The imperforate cryptocyst and slit-like opesiules exclude it from that genus. Although *S. fragilis* lacks gonoecia and vibracula, its original placement (Canu 1907*b*: 140) in *Setosella* seems to be correct. The species is represented in the Upper Bracklesham collection by the single fragment illustrated.

Canu's (1907*b*: pl. 19, fig. 15) restoration of the opesiules does not indicate their characteristically unequal lengths.

Distribution. Eocene (Lutetian); France.

Family **PORICELLARIIDAE** Harmer

Genus ***PORICELLARIA*** d'Orbigny

1854 *Poricellaria* d'Orbigny: 1106.
?1869*b* *Diplodidymia* Reuss: 468.

Type species (by original designation). *Poricellaria alata* d'Orbigny 1854: 1106. Eocene (Lutetian); vicinity of Paris, France.

Diagnosis. Frontal wall membranous, gymnocyst well developed. Cryptocyst completely developed, perforate or imperforate, with single or multiple, slit-like opesiule lying along one side only. Opesia small, terminal, semi-circular, oblique, approximately co-extensive with orifice. Avicularium adventitious, small, placed

Figs. 15–18. Figs. 15, 16. *Setosella fragilis* Canu. D.48468. Views of one zooecium and entire zoarial fragment. Fig. 17. *Poricellaria alata* d'Orbigny. D.48469. Frontal view of an internode fragment showing four rows of zooecia. Fig. 18. *Poricellaria alata* d'Orbigny. D.48470. View of reverse side of internode fragment with frontal surfaces hidden.

on proximal gymnocyst. Ovicell lacking. Zoarium erect, jointed, giving off basal rootlets. Internodes composed of 4 longitudinal rows of zooecia, one row on each face, but with orifices turned so as to open on the same face.

Remarks. The Eocene species of *Poricellaria*, including *P. alata*, *P. limanowskii* (Canu) (1907*b* : 143, pl. 19, fig. 8) and *P. vernoni* Cheetham (1963*b* : 52, pl. 1, figs. 7, 8), differ from the Oligocene–Recent species, including *P. complicata* (Reuss) (see Canu 1914*b* : 467, pl. 14, figs. 11, 12) and *P. ratoniensis* (Waters) (see Harmer 1926 : 314, pl. 23, figs. 3–8), in having the frontal surfaces of all zooecia hidden when the zoarium is viewed from the reverse side (see *P. alata*, Text-fig. 18), in having the opesia less oblique to the zooecial axis, and in having the avicularium proportionately smaller. These differences suggest that *Diplodidymia*, of which *P. complicata* is the type species, should possibly be reinstated as a subgenus for the Neogene forms.

Poricellaria alata d'Orbigny

(Text-figs. 17, 18)

1854 *Poricellaria alata* d'Orbigny : 1106.
?1886 *Cellularia diplodidymioides* Meunier & Pergens : 3, pl. 2, fig. 3.
1891 *Micropora articulata* Waters : 14, pl. 2, figs. 5, 6.
1907*b* *Diplodidymia alata* (d'Orbigny) Canu : 143, pl. 19, fig. 7.
?1907*b* *Diplodidymia crassomuralis* Canu : 144, pl. 19, fig. 6.
?1907*b* *Diplodidymia negrisi* Canu : 144, pl. 19, figs. 9, 10.
1933 *Diplodidymia alata* (d'Orbigny) ; Dartevelle : 74.
1935 *Diplodidymia alata* (d'Orbigny) ; Dartevelle : 112, text-fig. 1.
1946 *Diplodidymia alata* (d'Orbigny) ; Buge : 431.
?1946 *Diplodidymia crassomuralis* Canu ; Buge : 432.
?1946 *Diplodidymia negrisi* Canu ; Buge : 432.
1957 *Poricellaria alata* d'Orbigny ; Balavoine : 191.
1960 *Poricellaria alata* d'Orbigny ; Balavoine : 246.
1962 *Poricellaria alata* d'Orbigny ; Davis : 194.

Figured specimens. D.48469 (Text-fig. 17), D.48470 (Text-fig. 18).

Diagnosis. *Poricellaria* with frontal surfaces of all 4 zooecial rows visible in obverse aspect, reverse side showing basal surfaces of 2 rows ; opesial bisectrices of all rows make angles of 30°–45° with main axis ; proximal-gymnocystal avicularium small, placed obliquely ; opesiules single or double, distal one circular, proximal one slit-like.

Description. *Zoarium* erect, jointed. Internodes triangular in cross-section, with zooecia arranged in 4 longitudinal rows, all with frontal surface visible in obverse aspect, the zooecia of adjacent rows alternating in position. Proximal end of internode bluntly tapering, formed by 2 zooecia one of which is reduced and " membraniporoid ", the other normal but with a single, simple, proximal opening. Distal end not preserved.

Zooecia elongate club-shaped, asymmetrical, curved towards mid-line of obverse side. Zooecial length more than twice width. Gymnocyst about half zooecial length, smooth, convex, limited to proximal end of zooecium. Mural rim thin, sharp, smooth.

Cryptocyst completely developed, concave, deepest just proximal to opesia. Surface smooth, imperforate except for opesiule. Opesiule single or double, the distal one circular, the proximal one slit-like, placed on same side of cryptocyst, nearer zoarial mid-line (as viewed frontally).

Opesia semi-circular, oblique, its bisectrix making angles of 30°–45° with axis of internode. Proximal lip straight, as high as mural rim.

Avicularium adventitious, small, placed on proximal gymnocyst, the chamber oriented longitudinally and opening just below cryptocyst. Rostrum rounded, short, directed obliquely distally and outwards. Pivotal condyles or bar lacking. Proximal portion with a small pit or perforation.

Ovicell lacking.

Measurements :

Lz	(6) 0·453 (0·0276)	mm., 0·43–0·51 mm.
lz	(5) 0·185 (0·0167)	mm., 0·16–0·20 mm.
ho	(5) 0·068 (0·0086)	mm., 0·06–0·08 mm.
lo	(4) 0·086 (0·0000)	mm., 0·09 mm.
Lav	(4) 0·075 (0·0128)	mm., 0·06–0·09 mm.

Remarks. It is impossible to assess Dartevelle's interpretation (1935 : 112–114) of Meunier & Pergens's and Canu's species of *Poricellaria* as growth stages of *P. alata* until additional Lutetian and Montian material can be studied in detail. In the Recent *P. ratoniensis* the zooecia of the proximal internodes bear no resemblance to the normal, mature zooecia (see Harmer 1926, pl. 17, fig. 14), rather than being only slightly different as are *P. limanowskii, P. crassomuralis, P. negrisi, P. diplodidymioides* and *P. alata*. Preliminary study of specimens from the Sables de Fresville, Gourbesville (Manche), France (collected by Mr. Dennis Curry), suggests that *P. limanowskii*, at least, is a separate species from *P. alata*.

Waters's (1891 : 15) description of the avicularia of *P. alata* as vibracula was apparently based on his interpretation of the avicularian proximal pits as vibracular pores. Similar pits occur on the avicularia of *P. ratoniensis* (see Harmer 1926, pl. 23, figs. 6–8).

Distribution. ?Palaeocene (Montian) ; Belgium. Eocene (Lutetian) ; France. Eocene (Auversian) ; England. Eocene (Ludian) ; Italy.

Family **STEGANOPORELLIDAE** Hincks

Genus ***LABIOPORELLA*** Harmer

Labioporella*? *dartevellei[7] sp. nov.

(Text-figs. 19–22)

1851 " *Eschara fragilis* (Michelin), *non* Defrance " ; d'Orbigny : 344.
1907*b* " *Smittipora fragilis* (d'Orbigny) " ; Canu : 80, pl. 11, figs. 5–7.
?1933 *Steganoporella fragilis* Dartevelle : 74, pl. 2, fig. 2.

[7] After the late Edmond Dartevelle.

1946 " *Smittipora fragilis* (d'Orbigny) " ; Buge : 431.
1949 " *Smittipora fragilis* (d'Orbigny) " ; Balavoine : 773.
1956 " *Smittipora fragilis* (d'Orbigny) " ; Balavoine : 320, 324.
1957 " *Smittipora fragilis* (d'Orbigny) " ; Balavoine : 191.
1960 " *Smittipora fragilis* (d'Orbigny) " ; Balavoine : 246.
?1962 " *Smittipora fragilis* (d'Orbigny) " ; Gorodiski & Balavoine : 5.

HOLOTYPE. D.48471 (Text-figs. 19–21).

PARATYPES. D.48472 (Text-fig. 22), D.48473–75 (3 specimens), L.S.U. 8033.

DIAGNOSIS. *Labioporella* (?) with rudimentary zooecial dimorphism, the avicularian (?) zooecia differing only in size from the normal ones ; polypide tube short, wide, slightly eccentric ; mural rim smooth ; zoarium eschariform with edges bevelled owing to compression of zooecia of marginal rows.

DESCRIPTION. *Zoarium* erect, bilaminar, compressed, with zooecia arranged in 2–7 longitudinal rows on each side, those in adjacent rows alternating in position. Number of zooecial rows increases distally by bifurcation. Lateral margins of zoarium with bevelled appearance produced by compression of zooecia of marginal rows.

Zooecia rhomboidal to sub-rectangular, not markedly dimorphic, with evenly rounded distal borders, separated by a faint groove. Length about twice width. Mural rim smooth, thin and rather sharp distally, thicker and rounded proximally. Gymnocyst lacking.

Cryptocyst broad, fully developed, flat and shallow proximally, concave and steeply descending distally, evenly perforated with numerous, small, quincuncially arranged pores. Distal portion reflected upwards, except at lateral extremities, to form short, wide, slightly eccentric polypide tube with fully developed basal portion.

Opesia semi-circular, sub-terminal, with very narrow distal shelf. Opesiular indentations shallow, not well defined, unequal.

Avicularian (?) zooecia slightly larger than ordinary ones, but not different in form.

Ovicells lacking.

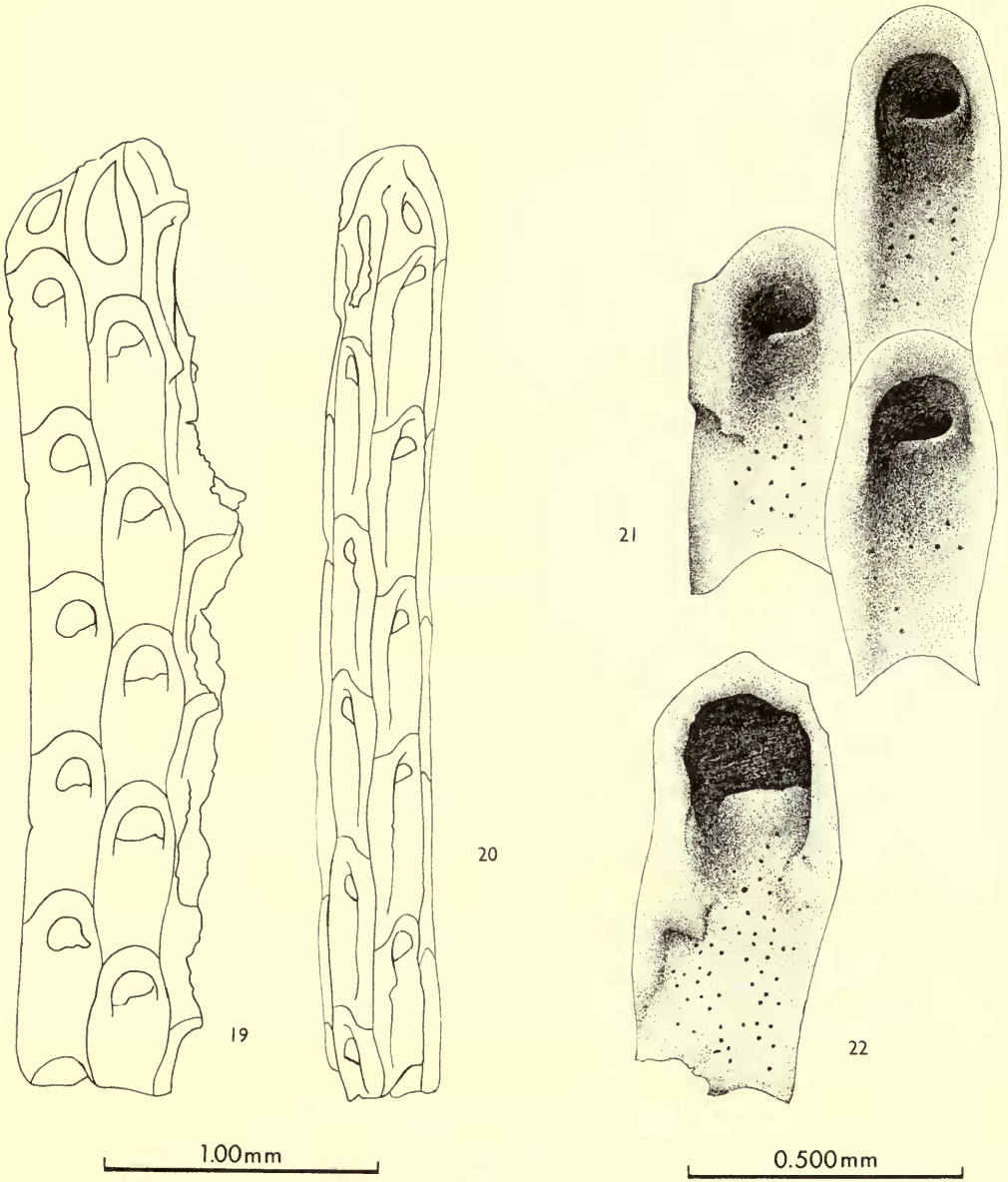
MEASUREMENTS :

Ordinary zooecia

Lz (9) 0·577 (0·0317) mm., 0·53–0·65 mm.
lz (9) 0·264 (0·0304) mm., 0·20–0·30 mm.
ho (6) 0·121 (0·0114) mm., 0·10–0·13 mm.
lo (6) 0·131 (0·0279) mm., 0·10–0·17 mm.

Avicularian (?) zooecia

Lz (2) 0·761 (0·0605) mm., 0·72–0·80 mm.
lz (2) 0·325 (0·0242) mm., 0·31–0·34 mm.
ho (1) 0·19 mm.
lo (1) 0·23 mm.



FIGS. 19–22. Figs. 19–21. *Labioporella? dartevellei* sp. nov. D.48471. Holotype. Front and edge views of fragmentary zoarium and details of three ordinary zooecia. Edge view shows bevelling produced by compression of marginal zooecia. Fig. 22. *Labioporella? dartevellei* sp. nov. D.48472. Paratype. Avicularian (?) zooecium.

Remarks. This widespread Eocene species has been a nomenclatorial puzzle for at least a hundred years since d'Orbigny mis-identified it with Michelin's (1845 : 176) material which he considered to have been in turn mis-identified with Defrance's (1828 : 428) species. Whether Michelin and Defrance had the same species or not, both of them had a different one from the present species : their illustrations show cylindrical, tubular zoaria with zooecia having sub-central opesiae. Canu (1907*b* : 80, pl. 11, figs. 5–7) re-described and, for the first time, illustrated d'Orbigny's material but, unfortunately, did not re-name it. Dartevelle (1933 : 74, pl. 2, fig. 2), who possibly had the same species, coined a new, but unfortunately homonymous, name for it.

French Lutetian specimens (Canu, 1907*b* : pl. 11, figs. 5–7) have many of the zooecia closed, especially along the zoarial margins, or with degenerated cryptocysts. Zooecia in the latter condition may represent fertile zooecia of the type noted by Cook (1964 : 51, 52) in various species of *Steganoporella* ; cryptocystal degeneration was not, however, noted by her in *Labioporella.*

This species does not fit well in either *Labioporella* or *Steganoporella* but seems closer to the former because of the asymmetrical polypide tube and the lack of a wide distal shelf in the avicularian (?) zooecia.

Distribution. Eocene (Lutetian) ; France, ?Senegal. ?Eocene (Auversian) ; Belgium.

Genus ***GAUDRYANELLA*** Canu

1900 *Gaudryanella* Canu : 380 (nomen nudum).
1907*b* *Gaudryanella* Canu : 141.

Type species (by monotypy). *Gaudryanella variabilis* Canu 1907*b* : 142, pl. 19, figs. 17–20. Eocene (Lutetian) ; vicinity of Paris, France.

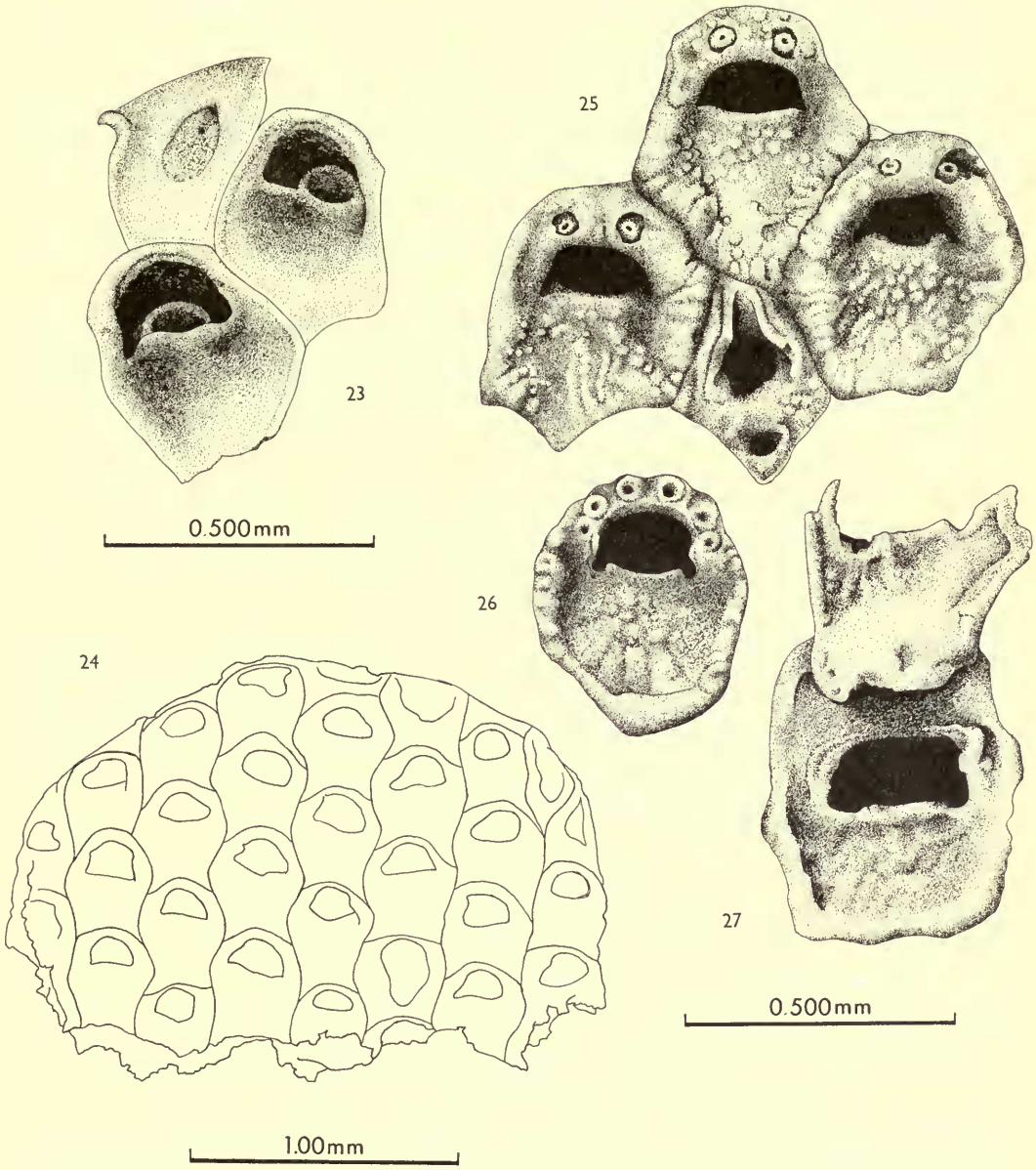
Diagnosis. Frontal wall membranous, gymnocyst lacking. Cryptocyst imperforate, fully developed, markedly concave, descending steeply to basal wall distally so as to form a small, eccentric polypide tube. Opesia large, terminal, with irregular, unequal opesiular indentations. Zooecial dimorphism not apparent. Ovicell lacking.

Remarks. The " large, ovarian zooecia ", mentioned by Canu (1907*b* : 141) in the original diagnosis, may have been formed through wear or degeneration of the cryptocyst. The absence of cryptocystal pores and zooecial dimorphism in this genus distinguishes it from *Steganoporella* and *Labioporella* ; the lack of a gymnocyst distinguishes it from *Siphonoporella.*

Gaudryanella variabilis Canu

(Text-figs. 23, 24)

1907*b* *Gaudryanella variabilis* Canu : 142, pl. 19, figs. 17–20.
1925 *Gaudryanella variabilis* Canu ; Canu : 47.
1946 *Steganoporella variabilis* (Canu) Buge : 432.
1956 *Gaudryanella variabilis* Canu ; Balavoine : 320, 324.
1957 *Steganoporella variabilis* (Canu) ; Balavoine : 191.
1960 *Gaudryanella variabilis* Canu ; Balavoine : 246.



FIGS. 23–27. Fig. 23. *Gaudryanella variabilis* Canu. D.48476. Two complete zooecia and a partially developed or degenerated one. Fig. 24. *Gaudryanella variabilis* Canu. D.48477. Fragmentary zoarium showing arrangement of zooecia. Fig. 25. *Entomaria dutempleana* (d'Orbigny). D.48482. Three mature zooecia and an avicularium. Fig. 26. *Entomaria dutempleana* (d'Orbigny). D.48483. A young zooecium with the spine bases not yet overgrown by conuli. Fig. 27. *Entomaria dutempleana* (d'Orbigny). D.48484. Ovicelled zooecium and part of the distal zooecium.

FIGURED SPECIMENS. D.48476 (Text-fig. 23), D.48477 (Text-fig. 24).

ADDITIONAL MATERIAL. Four specimens, D.48478–D.48481.

DIAGNOSIS. As for the genus (the only species).

DESCRIPTION. *Zoarium* uni- or bilaminar, erect, composed of wide fronds with zooecia arranged in 8 or more longitudinal rows, those in adjacent rows alternating in position.

Zooecia rhomboidal, rounded distally, straight proximally, separated by a very faint groove. Length and width subequal. Gymnocyst lacking. Mural rim thin, sharp, smooth, not distinctly raised.

Cryptocyst concave, deeply depressed at its distal end where it extends to basal wall to form a small, short, eccentric polypide tube. Surface smooth, imperforate.

Opesia large, asymmetrical, semi-circular, terminal. Opesiular indentations broad, shallow, unequal.

Heterozooecia and *ovicells* lacking.

MEASUREMENTS :

Lz (10) 0·363 (0·0345) mm., 0·32–0·40 mm.
lz (10) 0·354 (0·0474) mm., 0·27–0·44 mm.
ho (10) 0·131 (0·0128) mm., 0·11–0·14 mm.
lo (10) 0·189 (0·0272) mm., 0·15–0·21 mm.

REMARKS. The only suggestion of departure from the morphology of the ordinary zooecia in the Upper Bracklesham material is in a partially developed or degenerate zooecium (Text-fig. 23) in one fragment and several slightly reduced primoserial zooecia in another. None of these seems to fit the description given by Canu (1907*b* : 141) of " ovarian " zooecia.

DISTRIBUTION. Eocene (Lutetian) ; France.

Family **ASPIDOSTOMATIDAE** Jullien

Genus ***ENTOMARIA*** Duvergier

1921 *Entomaria* Duvergier : 150 (introduced in faunal list).
1927 " *Entomaria* Canu (*in* Duvergier) " ; Canu & Lecointre : 45.

TYPE SPECIES (by monotypy). *Rhagasostoma spiniferum* Canu 1914*b* : 469, pl. 15, fig. 7. Oligocene (Stampian) ; Gaas (Gironde), France.

DIAGNOSIS. Frontal wall membranous, gymnocyst narrow but encircling zooecium. Cryptocyst extensive, imperforate, merging with mural rim. Distal margin of mural rim with spine bases, often overgrown by conule-like extensions of distal gymnocyst. Opesia with lateral opesiular indentations and proximal cryptocyst-flange (= false polypide tube). Avicularia interzooecial, with opesiulated cryptocyst. Ovicell entozooecial.

REMARKS. This genus, often erroneously attributed to Canu (see Canu & Lecointre 1927 : 45), has been considered congeneric with *Lagarozoum* (see Bassler 1953 : 174),

from which it differs in lacking distinct cryptocyst ridges and in having oral spines, though these are often overgrown by projections of the distal gymnocyst forming structures similar to the conuli of *Lagarozoum* (see Harmer 1926 : 325, pl. 22, fig. 6). The ovicell of *Entomaria*, a typical entozooecial chamber opening above the opesia and extending distally under the gymnocyst and proximal part of the cryptocyst of the next zooecium, has been misinterpreted as entotoichal (see Canu & Lecointre 1927 : 45).

Entomaria dutempleana (d'Orbigny)

(Text-figs. 25–27)

1851 *Semieschara dutempleana* d'Orbigny : 366.
1900 *Rhagasostoma dutempleanum* (d'Orbigny) Canu : 428, pl. 7, figs. 22, 23.
1907*b* *Rhagasostoma dutempleanum* (d'Orbigny) ; Canu : 138, pl. 5, fig. 12.
1915 *Rhagasostoma dutempleanum* (d'Orbigny) ; Canu : 297.
1925 *Entomaria dutempleana* (d'Orbigny) Canu : 47.
1927 *Entomaria dutempleana* (d'Orbigny) ; Canu & Lecointre : 45.
1935 *Entomaria dutempleana* (d'Orbigny) ; Dartevelle : 115.
1937 *Entomaria dutempleana* (d'Orbigny) ; Dartevelle : 110.
1946 *Entomaria dutempleana* (d'Orbigny) ; Buge : 433.
1957 *Entomaria dutempleana* (d'Orbigny) ; Balavoine : 191.
1960 *Entomaria dutempleana* (d'Orbigny) ; Balavoine : 246.

Figured specimens. D.48482 (Text-fig. 25), D.48483 (Text-fig. 26), D.48484 (Text-fig. 27).

Additional material. Forty specimens, D.48485–D.48524.

Diagnosis. *Entomaria* with small zooecia and narrow gymnocyst ; ovicell small, without large lateral slits ; avicularia initiate new zooecial rows.

Description. *Zoarium* encrusting or erect, uni- or bilaminar, forming irregular, convoluted, hollow, tubular masses, the zooecia arranged more or less in longitudinal rows, those in adjacent rows alternating in position.

Zooecia ideally rhomboidal, straight sided, but often distorted or abortive, separated by distinct, sometimes deep furrows. Length and width subequal. Gymnocyst very narrow, but present entirely round zooecium. Mural rim wide, rounded, irregularly crenulated or beaded ; distal margin with 4–6 large, hollow spine bases, the more distal ones larger than the others ; distal gymnocyst grows over all but two of the spines to form a series of irregular hummocks or conuli. Zooecia communicate by simple pores placed near base of distal and lateral walls.

Cryptocyst extensive, covering nearly three-quarters of zooecial length. Surface nearly flat, highest near centre, deepest along lateral margins, imperforate, coarsely tuberculate, not distinctly marked off from mural rim. Distal part, along proximal lip of opesia, slightly raised to form a very narrow flange or false polypide tube.

Opesia semi-elliptical, much wider than high ; distal margin evenly and broadly rounded, provided with a very narrow distal shelf ; proximal margin scalloped, the broad cryptocystal flange limited on each side by a small, rounded opesiular indentation.

Avicularia interzooecial, initiating zooecial rows. Mural rim like that of zooecia but raised and pointed distally. Cryptocyst like that of zooecia but with one or two opesiules near proximal end. Opesia distal, oval. Spines and conuli absent.

Ovicell entozooecial, globular, opening over the opesia, the surface a tuberculate, imperforate awning projecting from the gymnocyst of the distal zooecium and discernible as a swelling under the proximal part of its gymnocyst. Ovicelled zooecia larger than ordinary ones, with larger opesia and without spines or conuli.

MEASUREMENTS :

Ordinary zooecia

Lz	(10) 0·494 (0·0623) mm.,	0·41–0·62 mm.
lz	(10) 0·423 (0·0417) mm.,	0·37–0·51 mm.
ho	(10) 0·122 (0·0274) mm.,	0·09–0·16 mm.
lo	(10) 0·208 (0·0202) mm.,	0·18–0·25 mm.

Ovicelled zooecia

Lz	(3) 0·596 (0·0623) mm.,	0·53–0·65 mm.
lz	(3) 0·445 (0·0534) mm.,	0·40–0·50 mm.
ho	(3) 0·140 (0·0049) mm.,	0·14–0·15 mm.
lo	(3) 0·242 (0·0178) mm.,	0·22–0·26 mm.

Avicularia

Lav	(7) 0·355 (0·0761) mm.,	0·27–0·48 mm.
lav	(7) 0·227 (0·0430) mm.,	0·17–0·29 mm.

REMARKS. Canu's description of the ovicell of this species as entotoichal (1925 : 47) cannot be verified in the present material. Though the opening of the ovicell is distal to the opesia, it is not far removed, and the ovicell chamber is immersed in the distal zooecium and covered by its gymnocyst and the proximal part of its cryptocyst.

DISTRIBUTION. Eocene (Lutetian) ; France, Belgium.

Family **FARCIMINARIIDAE** Busk

Genus ***NELLIA*** Busk

Nellia tenella (Lamarck)

(Text-fig. 28)

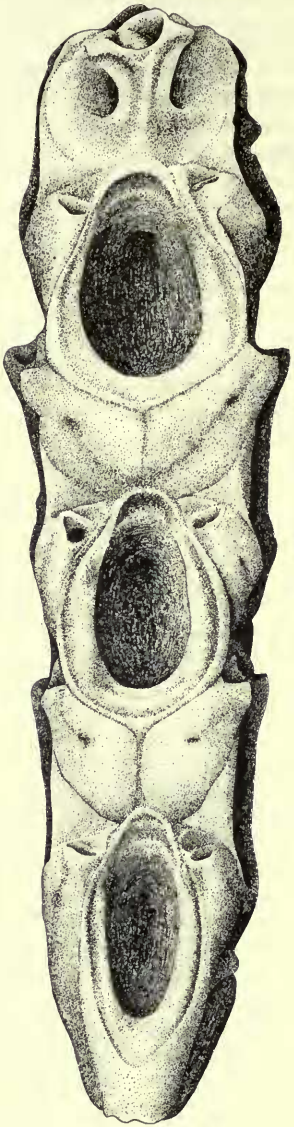
1816 *Cellaria tenella* Lamarck : 135.
1851 *Cellaria tenella* Lamarck ; d'Orbigny : 28.
1851 *Cellaria quadrilatera* d'Orbigny : 29.
1852*a* *Salicornaria dichotoma* Busk : 367 ; *non* Schweigger, 1819.
1852*b* *Nellia oculata* Busk : 18, pl. 64, fig. 6 ; pl. 65, fig. 4.
1873 *Nellia oculata* Busk ; Smitt : 3, pl. 1, figs. 53, 54.
1880 *Nellia oculata* Busk ; MacGillivray : 51, pl. 49, figs. 5, 5*a*, *b*.
1881 *Nellia oculata* Busk ; Haswell : 36.
1883 *Membranipora oculata* (Busk) Waters : 434.

1887 *Farcimia oculata* (Busk) Waters : 92.
1887 *Nellia oculata* Busk ; Hincks : 121.
1895 *Farcimia oculata* (Busk) ; MacGillivray : 50, pl. 6, figs. 6, 7.
1905 *Nellia oculata* Busk ; Thornely : 110.
1905 *Farcimia quadrilatera* (d'Orbigny) Waters : 3.
1907 *Nellia oculata* Busk ; Thornely : 185.
1907*b* *Farcimia tenella* (Lamarck) Canu : 76, pl. 10, figs. 36, 37.
1907*b* *Farcimia bituberculata* Canu : 73, pl. 10, figs. 24–29.
1909 *Farcimia oculata* (Busk) ; Waters : 167.
1909 *Nellia tenella* (Lamarck) ; Levinsen : 120, pl. 1, figs. 13 *a–e*.
1912 *Farcimia oculata* (Busk) ; Canu : 191, pl. 10, figs. 16, 19.
1913 *Farcimia oculata* (Busk) ; Waters : 489, pl. 67, figs. 8, 9.
1914 *Nellia oculata* Busk ; Osburn : 191.
1916 *Farcimia bituberculata* Canu ; Faura y Sans & Canu : 298.
1920 *Nellia bifaciata* Canu & Bassler : 197, pl. 32, figs. 15–19.
1920 *Nellia oculata* Busk ; Marcus : 5.
1921 *Farcimia tenella* (Lamarck) ; Duvergier : 8.
1921 *Farcimia oculata* (Busk) ; Robertson : 45.
1921 *Nellia oculata* Busk ; Marcus : 3.
1922 *Nellia oculata* Busk ; Marcus : 423.
1923 *Nellia oculata* Busk ; Canu & Bassler : 55, pl. 2, figs. 5–7.
1926 *Nellia oculata* Busk ; Harmer : 240, pl. 14, figs. 18–20.
1927 *Nellia oculata* Busk ; Osburn : 125.
1928 *Nellia oculata* Busk ; Canu & Bassler : 26.
1929*b* *Nellia oculata* Busk ; Canu & Bassler : 185, pl. 5, figs. 12, 13.
1932 *Nellia oculata* Busk ; Hastings : 410.
1934 *Nellia tenella* (Lamarck) ; Davis : 220.
1935 *Nellia oculata* Busk ; Dartevelle : 115.
1935 *Nellia bituberculata* (Canu) Dartevelle : 115.
1940 *Nellia oculata* Busk ; Osburn : 400.
1941 *Nellia oculata* Busk ; McGuirt : 66, pl. 2, fig. 5.
1941 *Nellia oculata* Busk ; Silén : 49.
1944 *Nellia ocullata* [sic] Busk ; Pokorny : 1–14.
1946 *Farcimia tenella* (Lamarck) ; Buge : 433.
1946 *Farcimia bituberculata* Canu ; Buge : 433.
1947 *Nellia oculata* Busk ; Osburn : 25.
1949 *Farcimia bituberculata* Canu ; Balavoine : 773.
1949 *Nellia oculata* Busk ; Vigneaux : 32, pl. 1, figs. 10–12.
1950 *Nellia oculata* Busk ; Osburn : 119, pl. 13, fig. 4.
1956 *Nellia tenella* (Lamarck) ; Balavoine : 321.
1957 *Nellia bituberculata* (Canu) ; Balavoine : 191.
1957 *Nellia tenella* (Lamarck) ; Cheetham : 93.
1959 *Nellia oculata* Busk ; Lagaaij : 482, text-fig. 1.
1960 *Nellia tenella* (Lamarck) ; Balavoine : 246.
1962 *Nellia tenella* (Lamarck) ; Cheetham : 326, pl. 1, figs. 4, 5.
?1962 *Nellia tenella* (Lamarck) ; Gorodiski & Balavoine : 6.
?1962 *Farcimia bituberculata* Canu ; Gorodiski & Balavoine : 6.
1962 *Nellia oculata* Busk ; Ghiurca, table 1.
1963 *Nellia tenella* (Lamarck) ; Braga : 27.
1963*b* *Nellia tenella* (Lamarck) ; Cheetham : 59, pl. 1, fig. 14.

FIGURED SPECIMEN. D.48525 (Text-fig. 28).

ADDITIONAL MATERIAL. Five specimens, D.48526–D.48530.

28



29

0.500mm

Diagnosis. *Nellia* with relatively narrow zooecia of same width on all 4 faces of zoarium ; avicularia paired, placed in proximo-lateral corners of gymnocyst, small, sometimes vestigial ; proximal end of internode with 1 large and 2 smaller pores ; distal end with 2 groups of such pores.

Description. *Zoarium* erect, delicate, articulated, dichotomously branching at nodes. Internodes long, slender, square in cross-section, the zooecia arranged in 4 longitudinal rows, those in adjacent rows alternating in position. Zooecia on all 4 faces subequal. Tips of articulating ends not preserved, but proximal portion consists of 2 normal and 2 greatly reduced zooecia.

Zooecia elongate, club-shaped, separated by distinct grooves. Length more than twice width. Gymnocyst smooth, convex, extending about a third of the zooecial length from the proximal margin. Mural rim smooth, sharp, slightly raised. Cryptocyst a narrow crescent on proximal margin of opesia ; surface smooth, slightly concave, imperforate.

Avicularia adventitious, small, paired except on zooecia just distal to reduced zooecia at proximal end of internode, placed in proximo-lateral corners of gymnocyst, the rostrum directed distally and slightly outwards. Pivotal structures lacking in material at hand. Proximal part of avicularian chamber sometimes with a small pore.

Ovicell entozooecial, discernible as a slight swelling under gymnocyst of distal zooecium. Frontal depression lacking in material at hand. Opesia of ovicelled zooecium slightly enlarged.

Measurements :

Ordinary zooecia

Lz	(8) 0·525 (0·0214) mm.,	0·50–0·56 mm.
lz	(8) 0·205 (0·0216) mm.,	0·17–0·24 mm.
ho	(8) 0·358 (0·0367) mm.,	0·32–0·41 mm.
lo	(8) 0·119 (0·0140) mm.,	0·10–0·14 mm.

Ovicelled zooecia

Lz	(1) 0·57 mm.	ho	(1) 0·42 mm.
lz	(1) 0·26 mm.	lo	(1) 0·18 mm.

Avicularia

Lav (10) 0·067 (0·0150) mm., 0·04–0·09 mm.

Remarks. Although it is true, as Harmer (1926 : 242) has remarked, that the description given by Lamarck (1816 : 135) for *Cellaria tenella* is insufficient to separate it from other jointed species, the probability that Lamarck had this ubiquitous

Figs. 28–29. Fig. 28. *Nellia tenella* (Lamarck). D.48525. One face of broken internode showing four complete zooecia and a broken one. Proximal zooecium is reduced ; distal complete zooecium is ovicelled. Fig. 29. *Nellia ventricosa* (Canu). D.48532. One face of broken internode showing three zooecia and a small portion of a fourth, distal one.

warm-water Cheilostome in his collection is very great. Moreover, even if Harmer was correct in discarding *C. tenella* from its synonymy, the next oldest available name is *C. quadrilatera* d'Orbigny, not *Nellia oculata* Busk.

Farcimia bituberculata Canu appears, from Canu's figures (1907*b*, pl. 10, figs. 24–29), to be the same as Harmer's (1926 : 242) " typical form " of *N. tenella* with vestigial avicularia.

The type specimens of *N. bifaciata* Canu & Bassler, U.S. National Museum Cat. Nos. 63954, 63955, have zooecia of different widths on different fragments, not on different faces of the same fragment, and are thus conspecific with *N. tenella*.

The Upper Bracklesham specimens differ from Recent *N. tenella* in having the functional avicularia without pivotal bar and the ovicell without the frontal depression (see Harmer 1926, pl. 14, figs. 19, 20 ; Osburn 1950, pl. 13, fig. 4). American Eocene specimens have the depression on the ovicell and some of the avicularia vestigial (see Cheetham 1962, pl. 1, figs. 4, 5).

Distribution. Eocene (Lutetian) ; France, Spain, ?Senegal. Eocene–Oligocene (Claibornian, Jacksonian, Vicksburgian) ; Gulf Coast of U.S.A. Miocene ; Egypt, Jamaica, Australia. Recent ; tropical and warm-temperate zones of all oceans.

Nellia ventricosa (Canu)

(Text-fig. 29)

1914*a* *Quadricellaria ventricosa* Canu : 298, pl. 4, figs. 6, 7.
?1962 *Nellia ventricosa* (Canu) Gorodiski & Balavoine : 6.

Figured specimen. D.48532 (Text-fig. 29).

Diagnosis. *Nellia* with short, stubby internodes, the proximal ends of which are formed by 2 opposing zooecia, each with a single, terminal opening ; gymnocyst and opesia of about equal length ; cryptocyst well developed ; avicularia large, paired, with chambers meeting on proximal gymnocyst and opening over opesiae of adjoining rows.

Description. *Zoarium* erect, jointed, probably branching at nodes. Internodes short, square in cross-section, with zooecia arranged in longitudinal rows, one row of 3–4 zooecia on each face, the zooecia of adjacent rows alternating in position. Proximal end of internode bluntly tapering, formed by 2 opposing zooecia narrower than more distal ones. One simple, terminal opening occurs at proximal end of each of the 2 proximal zooecia. Distal end of internode not well preserved.

Zooecia club-shaped, separated by furrows ; length nearly twice width. Gymnocyst about half zooecial length, arched, smooth, developed proximally only, covered in all but the proximal zooecia by enlarged avicularian chambers. Cryptocyst imperforate, smooth, well developed but narrow, horse-shoe shaped, limited to proximal and lateral margins ; not widened proximally. Surface of cryptocyst a smooth, horizontal shelf.

Opesia oval, more broadly rounded proximally, with a narrow shelf, lower than the cryptocyst, developed distally.

Avicularia adventitious, paired, with enlarged chambers meeting on mid-line of proximal gymnocyst and curving distally and outwards to open on disto-lateral margins of opesiae of adjoining rows. Rostrum short, pointed, directed proximally. Pivotal bar complete. Chamber with a distinct proximal pore.

Ovicell unknown.

MEASUREMENTS :

Lz (3) 0·581 (0·0226) mm., 0·56–0·60 mm.
lz (3) 0·319 (0·0522) mm., 0·27–0·38 mm.
ho (3) 0·359 (0·0171) mm., 0·34–0·38 mm.
lo (3) 0·185 (0·0430) mm., 0·14–0·23 mm.
Lav (4) 0·090 (0·0086) mm., 0·09–0·10 mm.

REMARKS. This species resembles *N. appendiculata* (Hincks) (Department of Zoology, British Museum (Natural History), 99.5.1.506, Hincks Collection) and *N. tenuis* Harmer (holotype, Department of Zoology, B.M. (N.H.), 28.3.6.62, Siboga Collection), Recent Indo-Pacific species, in zooecial size and shape, zoarial articulation, and avicularian size, shape, and position. Moreover, it appears to agree with *N. appendiculata* in having short, stubby internodes. Neither of the Recent species, however, has the avicularian chambers so enlarged as to meet over the proximal gymnocyst as they do in *N. ventricosa*, and further in both of those species the cryptocyst widens proximally. Harmer (1926 : 246) deemed differences of this magnitude sufficient to separate the two Recent species, so *N. ventricosa* should probably be maintained as a separate species.

N. midwayanica Canu & Bassler (1920 : 197, pl. 4, figs. 10–15), from the Palaeocene of the Gulf Coast of the U.S.A., differs from *N. ventricosa* in having longer internodes, less-developed avicularian chambers, and no distal shelf.

DISTRIBUTION. Eocene (Lutetian) ; France, ?Senegal.

Genus ***VINCULARIA*** Defrance

1829 *Vincularia* Defrance : 214.
1907*b* *Heterocella* Canu : 70 (objective).

TYPE SPECIES (by monotypy). *Vincularia fragilis* Defrance 1829 : 214, pl. 45, figs. 3, 3*a*, *b*. Eocene (Lutetian) ; vicinity of Paris, France.

DIAGNOSIS. Zoarium erect, probably articulated, the internodes quadriserial, slender, with 3 openings in each proximal end and 6 in each distal end. Zooecia dimorphic or trimorphic, similar zooecia occurring in 2 adjacent series : (1) *ordinary zooecia* (= " c-zooecia " of Canu 1907*b* : 71) small, with symmetrical opesiae ; (2) *avicularian* (*?*) *zooecia* (= " D-zooecia " of Canu) usually larger, with asymmetrical opesiae, outwardly curving distal margins, and usually distinct distal cryptocystal shelves ; and (3) *ovicelled zooecia* (lacking in some species) large, with symmetrical opesiae surmounted by the entozooecial ovicells. Zooecia of all three types with

membranous frontal wall, lacking gymnocyst. Cryptocyst a narrow, imperforate shelf round lateral and proximal margins of the large, oval opesia. Communication between zooecia of the same series by a large, median septule ; between zooecia of adjacent series by a septule connecting disto-lateral wall of one with proximo-lateral wall of the other. Small, single, adventitious avicularium present on mural rim of some species.

Remarks. Brown (1952 : 90, 91) remarked on the nomenclatorial inconsistency of declaring *Vincularia* an unrecognizable name while retaining its absolute junior synonym, *Heterocella* Canu (see Bassler 1935 : 125, 225).

The genus *Vincularia* apparently ranges from Middle to Upper Eocene (Lutetian, Auversian, Bartonian) both in England and on the Continent. It is yet unknown from America or, with certainty, from strata of Oligocene age. *Heterocella vicksburgica* Canu & Bassler (1920 : 198, pl. 82, figs. 11–14), from the Oligocene of Alabama, U.S.A. ; *Vincularia hians* Reuss and *V. haidingeri* Reuss (Kyri 1951 : 74, 75), from the Eocene (Ludian) of Rumania ; *Heterocella lerichei* Canu (1907*a* : 512, pl. 12, fig. 2), from the Oligocene (Stampian) and Miocene (Aquitanian) of France ; and *Heterocella pentagona* Canu & Bassler (1929*b* : 111, pl. 9, figs. 13–16), from the western Pacific, do not appear to have the avicularian (?) or " D " zooecia characteristic of the genus. Dartevelle (1942 : 149) stated that *Glauconome tetragona* Münster is " an undoubted " *Vincularia* but gave no evidence to support his claim. The six species included in the following table are the only ones which can at present be placed in the genus with certainty.

KEY TO SPECIES OF *VINCULARIA*

(Species named in square brackets are not described here.)

1 Zooecia trimorphic ; ovicelled zooecia present 2
Zooecia dimorphic ; ovicelled zooecia absent 4
2 Ovicelled zooecia greatly enlarged ; avicularian zooecia separated by a thread ; adventitious avicularia on zooecia of all three types . . ***V. monstruosa*** (Canu)
Ovicelled zooecia subequal to ordinary zooecia ; avicularian zooecia separated by a groove 3
3 Adventitious avicularia on ordinary and ovicelled zooecia only [***V. polymorpha*** (Canu)]
Adventitious avicularia on zooecia of all three types . . [***V. lediensis*** (Dartevelle)]
4 Adventitious avicularia present ; avicularian zooecia curved outwards strongly [***V. fragilis*** Defrance]
Adventitious avicularia absent ; avicularian zooecia curved outwards only slightly 5
5 Zooecia of both types slender, with elongate cryptocyst . . . ***V. davisi*** sp. nov.
Zooecia of both types obese, with short cryptocyst . . [***V. subsymmetrica*** (Canu)]

1. ***Vincularia monstruosa*** (Canu)

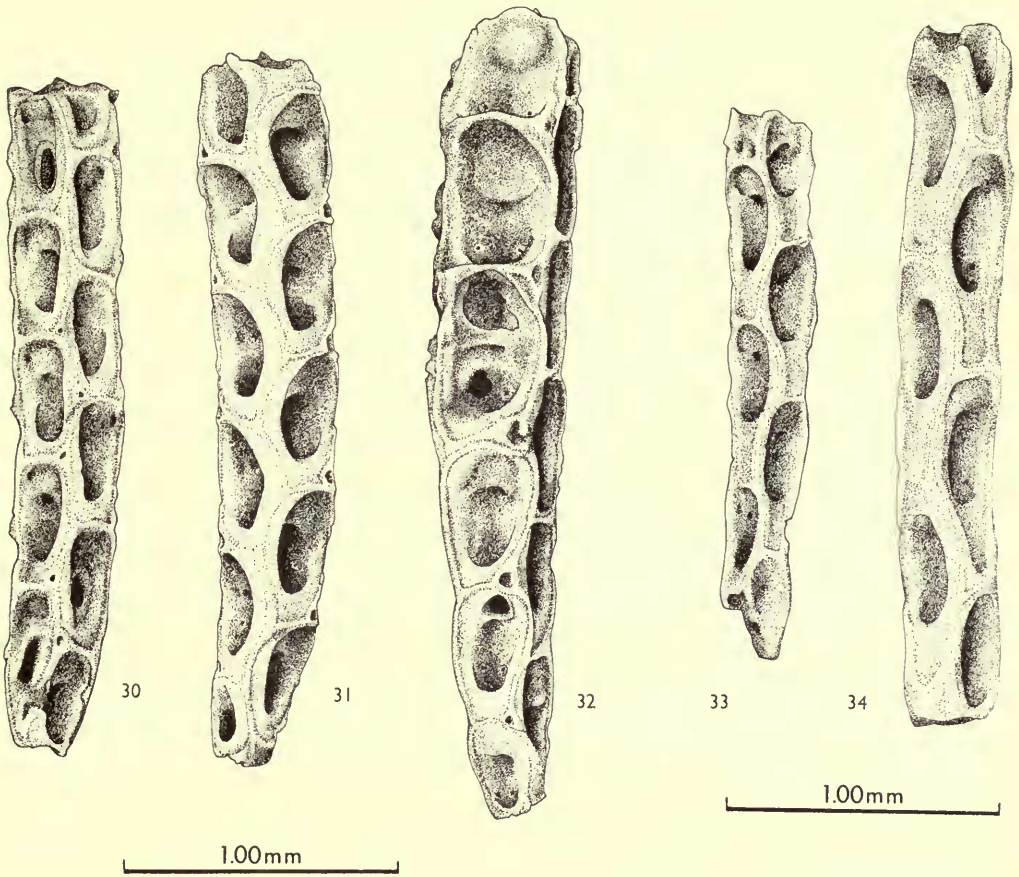
(Text-figs. 30–32)

1907*b* *Heterocella monstruosa* Canu : 71, pl. 10, figs. 11, 12.
1946 *Heterocella monstruosa* Canu : Buge : 430.
1956 *Vincularia monstruosa* (Canu) Balavoine : 324.
1960 *Vincularia monstruosa* (Canu) ; Balavoine : 246.
?1962 *Heterocella* sp., Davis : 194.

FIGURED SPECIMENS. D.48533 (Text-fig. 30), D.48534 (Text-fig. 31), D.48535 (Text-fig. 32).

ADDITIONAL MATERIAL. Ninety-one specimens, D.48536–D.48626.

DIAGNOSIS. *Vincularia* with trimorphic zooecia, the avicularian (?) ones curving away from each other markedly and separated by a thread ; ordinary and avicularian (?) zooecia both with very short cryptocysts ; adventitious avicularia at inner proximo-lateral angle of ordinary zooecia and at outer proximo-lateral angle of



FIGS. 30–34. Fig. 30. *Vincularia monstruosa* (Canu). D.48533. Internode fragment showing the two series of ordinary zooecia. Fig. 31. *Vincularia monstruosa* (Canu). D.48534. Internode fragment showing the two series of avicularian (?) zooecia. Fig. 32. *Vincularia monstruosa* (Canu). D.48535. Internode fragment showing a series of three avicularian (?) zooecia giving rise to a series of three ovicelled zooecia. Fig. 33. *Vincularia davisi* sp. nov. D.48627. Holotype. Internode fragment showing the two series of ordinary zooecia. The distal zooecium on the left has a pair of pores possibly associated with articulation. Fig. 34. *Vincularia davisi* sp. nov. D.48628. Paratype. Internode fragment showing the two series of avicularian (?) zooecia.

avicularian (?) and ovicelled zooecia ; ovicelled zooecia greatly enlarged, with well-developed entozooecial ovicells.

Description. *Zoarium* erect, probably articulated, composed of long, slender, curved internodes, tapering towards the base, lozenge-shaped in cross-section, the faces separated by obtuse angles having similar zooecia. Zooecia of adjacent rows alternate in position. Length of internode at least 7 zooecia. Proximal end of internode with 3 openings, 2 in avicularian (?) zooecia, 1 in ordinary zooecium. Distal end of internode with 6 openings, 2 in each of 2 avicularian (?) zooecia, 1 in each of 2 ordinary zooecia.

Ordinary zooecia rounded rectangular, separated by their narrow, smooth, rounded mural rims. Length about twice width. Interior very shallow, with a large, circular septule centrally, 2 similar ones disto-laterally, and 2 smaller ones near middle of lateral walls. Cryptocyst smooth, imperforate, slightly concave, forming a narrow, crescent-shaped shelf proximally and laterally. A similar, but deeper shelf runs distally from central septule to distal mural rim, sometimes connecting with the proximal cryptocyst to form a closure. Opesia oval, more broadly rounded distally than proximally, without differentiated indentations.

Avicularian (?) zooecia asymmetrically club-shaped, the longitudinal axes of those in one series curving strongly away from those of the other. Zooecia of both series separated by their narrow, smooth, rounded mural rims which are narrowest at the outer distal corner. Zooecial length twice width. Interior with same appearance and arrangement of pores as ordinary zooecia. Cryptocyst as in ordinary zooecia. Opesia as in ordinary zooecia but asymmetrical.

Ovicelled zooecia occur at distal end of series of avicularian (?) zooecia, rounded rectangular, larger than zooecia of other types, separated by narrow, rounded, smooth mural rims. Length slightly greater than width. Cryptocyst greatly reduced. Interior as in ordinary zooecia, except at distal end where distal wall is concave and slightly elevated, forming an entozooecial ovicell which extends slightly under cryptocyst of distal zooecium.

Avicularia adventitious, very small, single, placed proximo-laterally on mural rim with rounded rostrum directed distally and outwards. Ordinary zooecia with avicularium at inner proximal angle ; zooecia of other two types with avicularium at outer proximal angle.

Measurements :

Ordinary zooecia

Lz	(9)	0·440 (0·0350) mm., 0·36–0·47 mm.
lz	(10)	0·206 (0·0219) mm., 0·17–0·23 mm.
ho	(8)	0·346 (0·0330) mm., 0·27–0·38 mm.
lo	(10)	0·141 (0·0092) mm., 0·13–0·15 mm.
Lav	(9)	0·056 (0·0128) mm., 0·04–0·08 mm.

Avicularian (?) zooecia

Lz (10) 0·471 (0·0311) mm., 0·41–0·53 mm.
lz (9) 0·278 (0·0196) mm., 0·26–0·32 mm.
ho (10) 0·362 (0·0214) mm., 0·34–0·41 mm.
lo (9) 0·176 (0·0284) mm., 0·13–0·21 mm.
Lav (6) 0·078 (0·0084) mm., 0·07–0·09 mm.

Ovicelled zooecia

Lz (3) 0·522 (0·1150) mm., 0·39–0·61 mm.
lz (2) 0·415 (0·0191) mm., 0·40–0·43 mm.
ho (3) 0·504 (0·0964) mm., 0·39–0·56 mm.
Lav (1) 0·09 mm.

Remarks. It is very likely that this abundant Upper Bracklesham species is the one which Davis (1962 : 194) identified from Selsey as *Heterocella* sp.

Distribution. Eocene (Lutetian); France. ?Eocene (Auversian); England.

2. ***Vincularia davisi***[8] sp. nov.

(Text-figs. 33, 34)

Holotype. D.48627 (Text-fig. 33).

Paratypes. D.48628 (Text-fig. 34), D.48629–D.48640 (12 specimens), and L.S.U. 8034.

Diagnosis. *Vincularia* with dimorphic zooecia, the avicularian (?) ones curving away from each other only slightly so that they are not much different in form from the ordinary ones; avicularian (?) zooecia separated by threads; ordinary zooecia with very elongate proximal cryptocyst; adventitious avicularia and ovicells lacking.

Description. *Zoarium* erect, probably articulated, composed of long, very slender internodes, nearly square in cross-section; similar zooecia occur in each of the two adjacent series, alternating in position. Articulating ends of internodes not preserved.

Ordinary zooecia club-shaped, nearly three times as long as wide, separated by contiguous, broad, smooth, rounded mural rims. Interior shallow, with a large, circular, distal-median septule flanked on either side by a smaller one. Cryptocyst smooth, imperforate, slightly concave, forming a long shelf proximally and a very narrow one on each lateral margin. Distal wall without distinct shelf. Closures formed by proximal growth of a lamina from distal mural rim. Opesia oval, more broadly rounded distally than proximally, without opesiular indentations.

Avicularian (?) zooecia club-shaped, only slightly asymmetrical, the longitudinal axes of those in one series curving just perceptibly away from those in the other. Zooecia of the two series separated by their contiguous, smooth, rounded mural rims.

[8] After the late A. G. Davis.

Zooecial length two and a half times width. Septules as in ordinary zooecia. Cryptocyst as in ordinary zooecia, but wider laterally and continuing round distal margin of opesia in a broad shelf. Opesia oval, nearly symmetrical.

Adventitious *avicularia* and *ovicell* lacking.

Measurements :

Ordinary zooecia

Lz	(7) 0·602 (0·0517)	mm., 0·56–0·70 mm.
lz	(7) 0·211 (0·0128)	mm., 0·19–0·23 mm.
ho	(7) 0·372 (0·0119)	mm., 0·36–0·39 mm.
lo	(7) 0·130 (0·0134)	mm., 0·11–0·15 mm.

Avicularian (?) zooecia

Lz	(6) 0·789 (0·0515)	mm., 0·70–0·85 mm.
lz	(7) 0·300 (0·0277)	mm., 0·26–0·32 mm.
ho	(6) 0·370 (0·0467)	mm., 0·31–0·43 mm.
lo	(7) 0·145 (0·0131)	mm., 0·13–0·17 mm.

Remarks. This species is most closely related to the French Lutetian *V. subsymmetrica* (Canu) which it resembles in having dimorphic zooecia with the avicularian (?) zooecia only slightly curved and in lacking adventitious avicularia. The zooecia of *V. subsymmetrica* contrast with those of *V. davisi* in being obese and in having short cryptocysts.

Suborder ACANTHOSTEGA

Family **CRIBRILINIDAE** Hincks

Genus ***CRIBRILARIA*** Canu & Bassler

Cribrilaria parisiensis (Canu)

(Text-figs. 35, 36)

1913 " *Cribrilina puncturata* Busk " ; Canu : 148, pl. 4, fig. 3.
1926 *Cribrilina parisiensis* Canu : 751, pl. 27, fig. 1 ; pl. 29, fig. 6.
1929*a* *Cribrilina parisiensis* Canu ; Canu & Bassler : 37.
1933 *Cribrilina parisiensis* Canu ; Dartevelle : 106.
1936 *Cribrilina parisiensis* Canu ; Dartevelle : 29.
1954 *Cribrilina parisiensis* Canu ; Balavoine : 256.

Figured specimen. D.48641 (Text-figs. 35, 36).

Additional material. Four specimens, D.48642–D.48645.

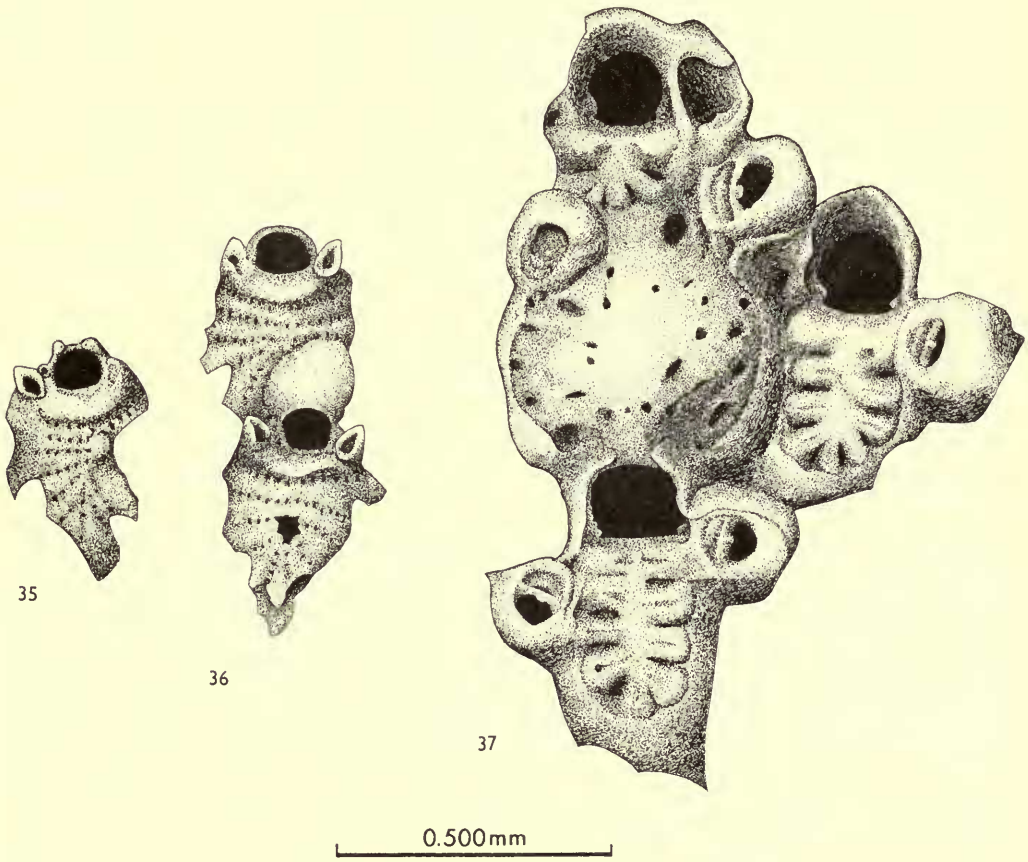
Diagnosis. *Cribrilaria* with paired adventitious avicularia and without distinct lumen pores ; ovicell without rim ; ovicelled zooecia without oral spines.

Description. *Zoarium* encrusting, unilaminar, the zooecia arranged in irregular longitudinal rows increasing in number distally by bifurcation. Zooecia in adjacent rows alternate in position.

Zooecia elliptical, separated by distinct grooves. Length about one and a half times width. Frontal shield convex, highest at sub-oral umbo, without definite gymnocyst. Costae 8–11 excluding apertural bar, narrow, smooth, tapering towards centre of shield, without distinct lumen pores. Lacunae small, circular or elliptical, 6 or rarely 5 between adjacent costae. Apertural bar about half as wide again as costae, not tapering, strongly curved, with a projecting, central umbo which is concave on both distal and proximal sides.

Orifice terminal on frontal surface, small, semi-circular, the proximal lip slightly concave. Distal margin with 4 erect, hollow spine bases (lacking in ovicelled zooecia).

Avicularia adventitious, small, paired, frontal, placed one on either side of orifice, the rostrum directed distally and outwards. Rostrum short, pointed. Complete pivotal bar sometimes preserved.



FIGS. 35–37. Figs. 35, 36. *Cribrilaria parisiensis* (Canu). D.48641. A non-ovicelled zooecium and two other zooecia, the proximal one ovicelled, in different parts of the same fragmentary zoarium. Fig. 37. *Membraniporella radiata* (Reuss). D.48646. Three zooecia, the proximal one ovicelled.

Ovicell hyperstomial, globular, nearly circular in frontal outline. Surface smooth, imperforate, without rim. Opening nearly perpendicular to zooecial orifice, small, semi-circular.

MEASUREMENTS :

Lz (8) 0·316 (0·0183) mm., 0·30–0·34 mm.
lz (8) 0·252 (0·0323) mm., 0·20–0·30 mm.
ho (9) 0·057 (0·0060) mm., 0·05–0·07 mm.
lo (9) 0·092 (0·0071) mm., 0·09–0·10 mm.
Lav (7) 0·055 (0·0068) mm., 0·05–0·07 mm.
Lov (6) 0·140 (0·0070) mm., 0·13–0·14 mm.

REMARKS. This species does not fit easily in any known Cribrilinid genus. The frontal shield, including the absence of a gymnocyst, the orifice, and the ovicell are very much like those of *Eschara radiata* Moll, the type species of *Cribrilaria*, which has vicarious, rather than adventitious avicularia.[9] The avicularia of *C. parisiensis* are quite like those of *Lepralia gattyae* Busk, the type species of *Puellina*, which has a different frontal shield. By analogy with other Acanthostega, e.g. *Castanopora* (see Larwood 1962 : 203–206), greater systematic weight is placed on the form of the frontal shield than on the position of the avicularia.

C. parisiensis differs from the eastern European Upper Eocene species, *C. calomorpha* (Reuss), in number of costae and form of orifice (see Malecki 1963 : 115).

DISTRIBUTION. Eocene (Auversian) ; Belgium, France. Eocene (Bartonian) ; Belgium. Oligocene (Stampian) ; France.

Genus ***MEMBRANIPORELLA*** Smitt

1873 *Membraniporella* Smitt : 10.

TYPE SPECIES (selected by Hincks 1877). *Lepralia nitida* Johnston 1838 : 277, pl. 34, fig. 7. Recent ; British Isles.

DIAGNOSIS. Frontal shield composed of relatively few costae over-arching a well-developed membrane. Gymnocyst prominent proximally and laterally. Costae usually with conspicuous, open lumina. Lacunae slit-like and undivided or with few lateral fusions. Orifice semi-circular to sub-circular, sometimes with lateral condyles. Distal spines frequently present. Avicularia, where present, adventitious, placed usually on proximal part of gymnocyst near orifice of laterally adjacent zooecium. Ovicell hyperstomial, imperforate in the type species, elongate globular. Orifice of ovicelled zooecia slightly wider than that of non-ovicelled ones.

REMARKS. Though the diagnosis given here is based in large part on the type species, *L. nitida* (holotype, Department of Zoology, British Museum (Natural History), 47.9.16.66, Johnston Collection), it has been framed to embrace the extremes

[9] *C. calomorpha* (Reuss) (Malecki 1963 : 115), from the Ludian of Poland and Rumania, also has paired adventitious avicularia ; *C. simulator* (Canu & Bassler 1920 : 298, pl. 41, fig. 21 ; pl. 84, fig. 14), from the Upper Eocene and Oligocene of the Gulf Coast of the U.S.A., has paired adventitious avicularia on the ovicelled, but not the ordinary zooecia.

of variation shown by *M. aragoi* (Audouin) (see Harmer 1926, pl. 34, figs. 12–14) and *M. compressa* Canu & Bassler (1920, pl. 41, figs. 6–8). Such species as *M. radiata* (Reuss), described below, and *M. planula* Canu & Bassler (1920, pl. 5, figs. 8–10), *M. ulrichi* Canu & Bassler (1920, pl. 41, figs. 4, 5), *M. monilifera* Canu & Bassler (1920, pl. 41, figs. 9, 10), *M. bioculata* Canu & Bassler (1920, pl. 41, figs. 11–13), and *M.? subagassizi* Canu & Bassler (1920, pl. 84, figs. 8–13) seem to be much closer to the type species.

Membraniporella radiata (Reuss)

(Text-fig. 37)

1869*a* *Celleporaria radiata* Reuss : 292, pl. 30, fig. 9.
1885 *Cribrilina chelys* Koschinsky : 36.
1889 *Cribrilina chelys* Koschinsky ; Pergens : 70.
1891 *Cribrilina chelys* Koschinsky ; Waters : 16, pl. 2, fig. 10.
1898 *Cribrilina chelys* Koschinsky ; Neviani : 39, text-fig. 1.
1907*b* *Cribrilina chelys* Koschinsky ; Canu : 145, pl. 20, fig. 1.
1929*a* *Collarina radiata* (Reuss) Canu & Bassler : 34, pl. 2, figs. 17, 18.
1933 *Collarina radiata* (Reuss) ; Dartevelle : 101.
1946 *Cribrilina chelys* Koschinsky ; Buge : 433.
1951 *Collarina radiata* (Reuss) ; Kyri : 74.
1962 *Collarina radiata* (Reuss) ; Ghiurca, table 1.

Figured specimen. D.48646 (Text-fig. 37).

Additional material. Three specimens, D.48647–D.48649.

Diagnosis. *Membraniporella* with 5–7 costae in addition to the apertural bar and without lateral fusions ; costae with exposed, slit-like lumina ; orifice with lateral condyles ; avicularia adventitious, single, paired, or multiple on the lateral gymnocyst and, occasionally, vicarious as well ; ovicell large, coarsely perforate.

Description. *Zoarium* erect, bilaminar, compressed, the zooecia arranged in irregular, alternating, longitudinal rows.

Zooecia irregularly elliptical, nearly twice as long as wide, separated by furrows. Gymnocyst wide, especially proximally, strongly arched, smooth. Frontal shield relatively flat, small, barely twice the size of the orifice. Costae 5–7 (usually 7) excluding apertural bar, short, broad, triangular, smooth, each with a single, slit-like, exposed lumen. Adjacent costae without lateral fusions, separated by a single, slit-like lacuna. Median line of shield with thin, smooth, irregular ridge formed by fusion of ends of costae. Apertural bar formed by a pair of opposing costae slightly thicker than the others.

Orifice sub-circular, less rounded proximally than distally, with a pair of stout, deeply placed lateral condyles close to proximal margin. Peristome short, thin, present distally only. Oral spines lacking.

Avicularia adventitious, single, paired, or, rarely, multiple, placed on lateral gymnocyst proximal to orifice in such position as to be near orifice of zooecium of adjacent row. Rostrum umbo-like, rounded, directed upwards, outwards, and

slightly distally or proximally. Pivotal bar complete, with small, rounded knob on rostral side.

Vicarious avicularia lacking in specimens at hand.

Ovicell hyperstomial, larger than zooecia, globular, with coarsely perforate surface. Orifice of ovicelled zooecia semi-circular, wider than that of ordinary zooecia, with weaker condyles and better-developed distal peristome.

Measurements :

Ordinary zooecia

Lz (5) 0·575 (0·0237) mm., 0·56–0·62 mm.
lz (6) 0·304 (0·0438) mm., 0·23–0·34 mm.
ho (5) 0·147 (0·0140) mm., 0·14–0·17 mm.
lo (6) 0·144 (0·0183) mm., 0·13–0·17 mm.
Lav (7) 0·171 (0·0086) mm., 0·16–0·19 mm.

Ovicelled zooecia

lo (5) 0·190 (0·0164) mm., 0·17–0·21 mm.
Lov (5) 0·498 (0·0299) mm., 0·44–0·51 mm.

Distribution. Eocene (Lutetian) ; France, Germany. Eocene (Auversian) ; Belgium. Eocene (Ludian) ; Poland, Italy, Rumania.

Suborder ASCOPHORA

Family **EXECHONELLIDAE** Harmer

Genus ***EXECHONELLA*** Duvergier

1924 *Exechonella* Duvergier : 18.

Type species (by monotypy). *Cyclicopora? grandis* Duvergier 1921 : 124, pl. 3, figs. 2, 3. Miocene (Aquitanian) ; Gironde, France.

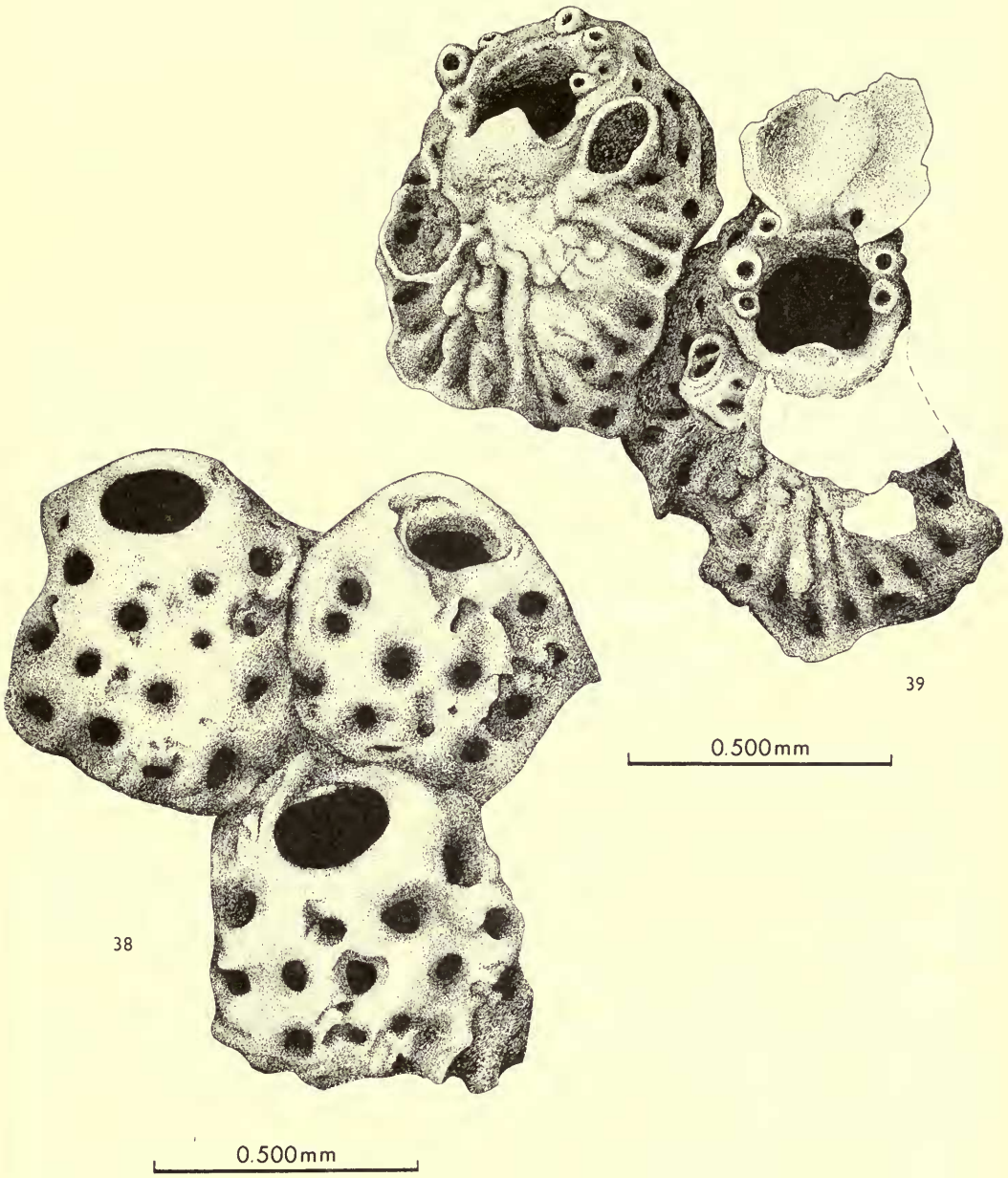
Diagnosis. Frontal wall calcareous, over-arching a fully developed membrane. Frontal pores large, irregularly dispersed over surface, not filled with tissue. Peristome long or short, tubular, with small lateral denticles or none. Secondary orifice sub-circular. Avicularia, where present, adventitious, frontal, with pointed rostrum and pivotal bar. Ovicells usually lacking ; where present, small, developed on distal side of peristome.

Remarks. This genus is usually attributed to Canu & Bassler (1927 : 4), who selected as type species *Hiantopora magna* MacGillivray (see Harmer 1957 : 652). However irregular, Duvergier's introduction of the genus has priority, with *C.? grandis* the type species by monotypy.

Exechonella sp.

(Text-fig. 38)

Figured specimen. D.48650 (Text-fig. 38).



FIGS. 38–39. Fig. 38. *Exechonella* sp. D.48650. Three zooecia from the small zoarial fragment. Fig. 39. *Hippopleurifera canui* nom. nov. D.48651. Two zooecia, the one on the right ovicelled, from the small zoarial fragment.

DESCRIPTION. *Zoarium* presumably encrusting, the basal surface uncalcified.

Zooecia irregularly elliptical, separated by shallow, poorly defined grooves. Length and width subequal. Frontal wall strongly inflated, thick, smooth, with 12–15 large, circular, quincuncially arranged foramina.

Peristome short, the secondary orifice terminal on frontal surface, sub-circular, slightly wider than long, without denticles.

Avicularia and *ovicells* lacking in specimen at hand.

MEASUREMENTS :

Lz	(4) 0·614 (0·0237) mm., 0·55–0·68 mm.	
lz	(4) 0·603 (0·0386) mm., 0·56–0·65 mm.	
ho	(4) 0·141 (0·0164) mm., 0·12–0·15 mm.	} secondary orifice
lo	(4) 0·214 (0·0209) mm., 0·19–0·24 mm.	} secondary orifice

REMARKS. Only one fragment, badly worn and consisting of just 7 zooecia, recovered from the Upper Bracklesham material, is referable to *Exechonella*. Absence of positive characters, probably a consequence of its poor preservation, makes specific assignment impossible.

Family **UMBONULIDAE** Canu

Genus ***HIPPOPLEURIFERA*** Canu & Bassler

Hippopleurifera canui[10] nom. nov.

(Text-fig. 39)

1873 *non Hippothoa mucronata* Smitt : 45, pl. 8, fig. 169.
1914*a* *Petralia mucronata* Canu : 301, pl. 4, fig. 5 (misspelt " *micronata* ").

FIGURED SPECIMEN. D.48651 (Text-fig. 39).

DIAGNOSIS. Unilaminar, probably encrusting *Hippopleurifera*, with large, mucronate zooecia ; areolae in a single row ; orifice with feeble condyles and 6 distal spines on non-ovicelled and 4–6 on ovicelled zooecia ; avicularium single or paired, lateral sub-oral, with rostrum directed proximally and inwards.

DESCRIPTION. *Zoarium* unilaminar, probably encrusting.

Zooecia rhomboidal, separated by a shallow groove. Length nearly one and a half times width. Frontal wall thick, very convex, highest at mucro. Surface coarsely tuberculate centrally, areolate in a single row marginally, with inter-areolar costules nearly reaching centre.

Orifice large, terminal, inclined distally, hidden by a large, projecting mucro proximally, rounded sub-quadrate, with a pair of feeble condyles near proximal corners of lateral margins. Distal margin with 6 large, hollow spine bases on both ovicelled and non-ovicelled zooecia, in material at hand.

[10] After the late Ferdinand Canu.

Avicularium adventitious, frontal, single in material at hand, placed near proximo-lateral margin of orifice with rostrum directed upwards, proximally, and slightly inwards. Rostrum rounded, pivotal bar complete.

Ovicell hyperstomial, globular, elongate. Surface not preserved in specimen at hand.

MEASUREMENTS :

Lz (2) 0·821 (0·0242) mm., 0·80–0·84 mm.
lz (2) 0·611 (0·0181) mm., 0·60–0·62 mm.
ho (2) 0·222 (0·0121) mm., 0·21–0·23 mm.
lo (2) 0·214 (0·0242) mm., 0·20–0·23 mm.

REMARKS. Canu (1914*a* : 301) described the ovicell of this species as having crescents incompletely calcified on their edges, but in his figure (pl. 4, fig. 5) the surface of the ovicell appears smooth. The specimen illustrated by Canu has 4 spines on the ovicelled zooecia in contrast to the 6 (one overlapped by the floor of the ovicell) displayed by the Upper Bracklesham specimen. Canu characterized the species as having paired avicularia, but his figure shows only one zooecium with two avicularia. One of the zooecia in the Upper Bracklesham specimen may have a small remnant of a second avicularium.

This species is represented in the Curry Collection by the single specimen of two almost complete and one fragmentary zooecia.

DISTRIBUTION. Eocene (Lutetian) ; France.

Family **EXOCHELLIDAE** Bassler

Genus ***ESCHAROIDES*** Milne Edwards

1836 *Escharoides* Milne Edwards : 218.
1902 *Peristomella* Levinsen : 26.

TYPE SPECIES (chosen by Norman 1903). *Cellepora coccinea* Abildgaard 1806 : 30, pl. 146, figs. 1, 2. Recent ; North Sea, Heligoland.

DIAGNOSIS. Frontal wall calcareous, granular to tuberculate, with a single row of marginal areolae separated by short, peripheral costules. Orifice sub-circular, deeply buried in peristome, steeply inclined distally, with a short, curved plate projecting into the zooecium from its distal margin. Peristome not differentiated from frontal surface, sometimes with distal spines. Secondary orifice oval, usually with a median-proximal denticle, and sometimes with a pair of proximo-lateral ones as well. Avicularia adventitious, usually paired, placed on lateral margins of frontal near proximal part of peristome. Rostrum usually pointed, directed outwards and distally. Pivotal bar complete. Larger, vicarious avicularia, with swollen chamber margined with areolae, sometimes present. Ovicell hyperstomial, globular, with marginal areolae separated by costules, and, at least in some species, with finer perforations in radial lines between costules. Interzooecial communication by pore-chambers. Operculum a weakly chitinized valve.

Remarks. Brown's suggestion (1952 : 298) that species of *Escharoides* with well-developed marginal areolae on the ovicells may have to be transferred to a new genus need not be followed, for specimens of the type species (e.g. Department of Zoology, British Museum (Natural History), 99.5.1.858, 91.8.7.16, 93.8.7.31, and 1950.11.6.4) show ovicells with distinct areolae. Most species of *Escharoides* have pointed, not spatulate avicularia (cf. Brown 1952 : 297).

Escharoides aliferus (Reuss)

(Text-figs. 40, 41)

1869*a* *Eschara alifera* Reuss : 274, pl. 33, fig. 11.
1887 *Eschara alifera* Reuss ; Pergens : 7.
1889 *Mucronella alifera* (Reuss) Pergens : 71.
1891 *Smittia coccinea* var. *alifera* (Reuss) ; Waters : 21, pl. 3, fig. 7.
1908 *Peristomella alifera* (Reuss) Canu : 92, pl. 7, fig. 7.
1925 *Peristomella alifera* (Reuss) ; Canu : 47.
1946 *Escharoides aliferus* (Reuss) Buge : 434.
1949 *Peristomella alifera* (Reuss) ; Balavoine : 774.
1957 *Escharoides aliferus* (Reuss) ; Balavoine : 191.
1960 *Romancheina gouetensis* Balavoine : 247, pl. 6, figs. 11–14 ; pl. 7, figs. 1–4.
1962 *Escharoides aliferus* (Reuss) ; Ghiurca, table 1.
1963 *Escharoides aliferus* (Reuss) ; Braga : 34.

Figured specimens. D.48652 (Text-fig. 40), D.48653 (Text-fig. 41).

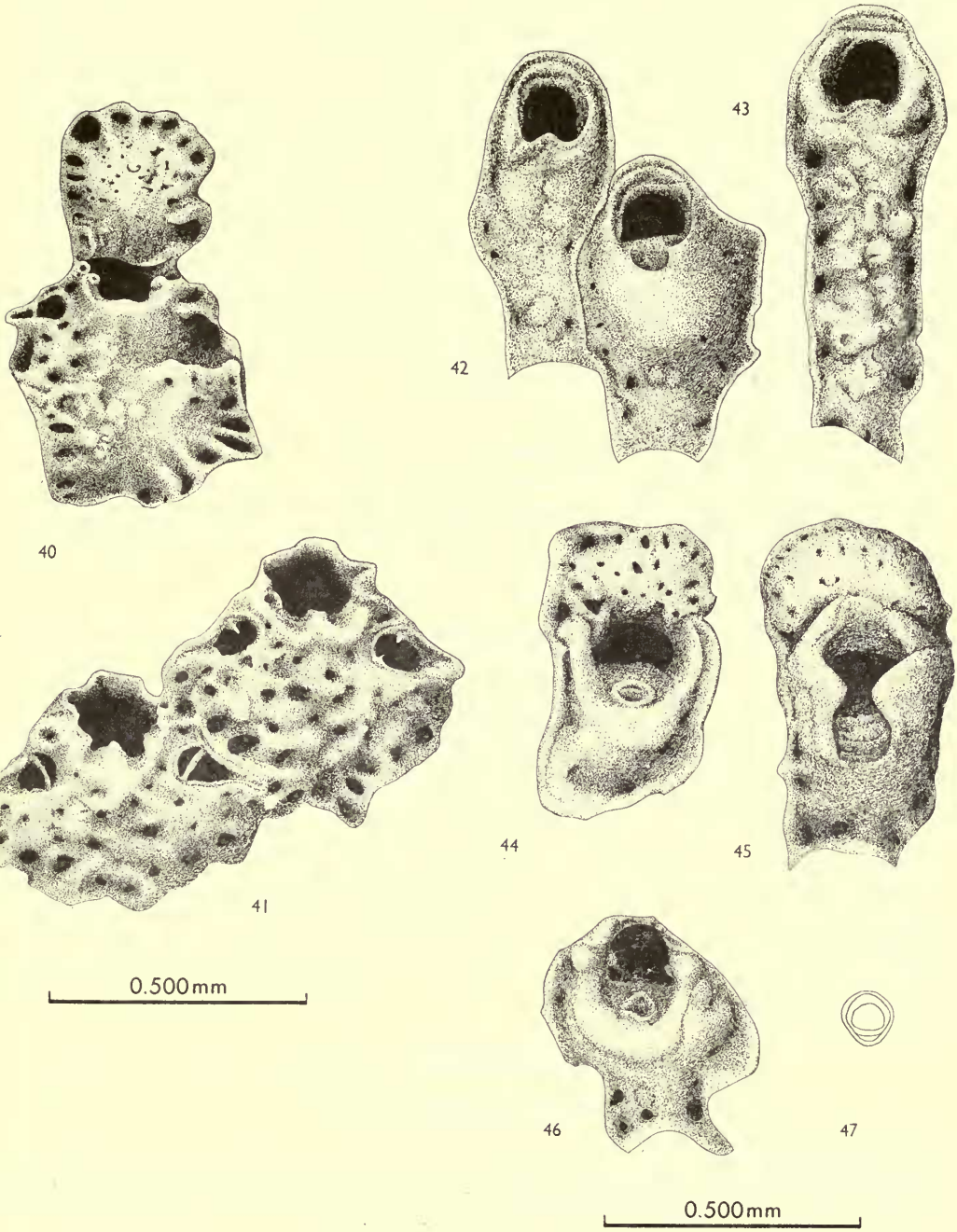
Additional material. Twenty-two specimens, D.48654–D.48675.

Diagnosis. Erect, bilaminar *Escharoides* with prominent mucro flanked by a smaller denticle on either side ; a single spine base at each lateral margin of secondary orifice ; avicularia paired, occupying swollen chambers at lateral margins of frontal ; ovicell elongate, irregularly perforated, areolated.

Description. *Zoarium* erect, arborescent, arising from an encrusting base, composed of compressed, bilaminar fronds with more than 12 longitudinal rows of zooecia on each side ; the zooecia in adjacent rows alternate in position. Inter-zooecial communication by small pore-chambers in distal and disto-lateral walls.

Zooecia irregularly rhombic, rounded distally, the lateral avicularia forming wing-like expansions on the sides. Zooecia separated by shallow, ill-defined depressions. Zooecial length almost one and a half times width. Frontal wall moderately thick, convex, highest at proximal lip of secondary orifice. Surface smooth except for

Figs. 40–47. Fig. 40. *Escharoides aliferus* (Reuss). D.48652. Ovicelled zooecium. Fig. 41. *Escharoides aliferus* (Reuss). D.48653. Two non-ovicelled zooecia. Fig. 42. *Smittoidea variabilis* (Canu). D.48676. Two zooecia from a bilaminar fragment. The one on the right has an avicularium. Fig. 43. *Smittoidea variabilis* (Canu). D.48677. A zooecium from another bilaminar fragment in a more advanced state of calcification. Fig. 44. *Smittoidea variabilis* (Canu). D.48678. An ovicelled zooecium from a unilaminar fragment. Fig. 45. *Smittoidea variabilis* (Canu). D.48679. An ovicelled zooecium from another unilaminar fragment. The peristome is unusually developed. Figs. 46, 47. *Smittoidea variabilis* (Canu). D.48679. A zooecium and the outline of an avicularium of another zooecium from the same unilaminar fragment.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large, irregular tubercles along mid-line and prominent peripheral costules separating the areolae. Areolae large, sub-circular or elliptical, evenly spaced in a row of 18–25 round lateral and proximal margins. Additional, smaller areolae, 4–6, on line separating avicularian chamber from frontal surface.

Orifice small, sub-circular, inclined distally, deeply buried in peristome. Distal plate well developed, with straight margin and concave surface. Peristome not differentiated from frontal surface, thin, with a small, hollow spine base at mid-point of each lateral margin. Secondary orifice inclined distally, roughly circular, with large, median mucro flanked on either side by a much smaller denticle.

Avicularia adventitious, but nearly of interzooecial position, paired, occupying large, slightly swollen chambers on lateral margins of zooecia just proximal to orifice. Rostrum pointed, attenuated, directed transversely outwards. Pivotal bar complete.

Ovicell hyperstomial, globular, elongate, opening broadly into peristome, the lip of the ovicell forming a convex projection into secondary orifice. Surface convex, irregularly perforated with numerous small pores between radiating, costule-like ridges. Orifice of fertile zooecium not modified.

Measurements :

Lz	(7) 0·552 (0·0640) mm., 0·47–0·68 mm.	
lz	(6) 0·398 (0·0461) mm., 0·35–0·48 mm.	
ho	(5) 0·123 (0·0167) mm., 0·10–0·14 mm.	secondary orifice
lo	(5) 0·176 (0·0076) mm., 0·17–0·19 mm.	secondary orifice
Lav	(7) 0·184 (0·0396) mm., 0·14–0·26 mm.	
Lov	(2) 0·321 (0·0302) mm., 0·30–0·34 mm.	

Remarks. Balavoine (1960 : 246) included this species in his list from the Lutetian of Bois-Gouët (Loire-Atlantique) with the annotation that Canu (1908) had found it, but that it was missing from his (Balavoine's) material. At the same time he (1960 : 247) described *Romancheina gouetensis* as a new species similar to *E. aliferus* but having a uniformly perforate (" tremocystal ") frontal. His figures (1960 : pl. 6, figs. 11–14 ; pl. 7, figs. 1–4) show, however, not tremopores but areolae in the double lateral rows characteristic of the frontal of *E. aliferus* where it is joined by the avicularian chambers. Thus there is little doubt that Balavoine's species is the one correctly identified by Canu with *E. aliferus*.

The pore-chambers of the Upper Bracklesham specimens are very small and difficult to identify.

Distribution. Eocene (Lutetian) ; France. Eocene (Ludian) ; Italy, Hungary, Poland, Rumania.

Family **SMITTINIDAE** Levinsen

Genus ***SMITTOIDEA*** Osburn

1952 *Smittoidea* Osburn : 408.

Type species (by original designation). *Smittoidea prolifica* Osburn 1952 : 408, pl. 48, figs. 7, 8. Recent ; Californian coast, U.S.A.

Diagnosis. Frontal wall calcareous, smooth, granular, or tuberculate, with a single row of marginal areolae proximally and laterally. Orifice sub-circular to semi-circular with well-developed condyles and a median proximal lyrula. Peristome high distally and laterally, usually with a proximal notch ; spines, if present, evanescent. Avicularium adventitious, frontal, median sub-oral, placed within peristomial sinus or just proximal to it, rostrum directed longitudinally proximally. Ovicell hyperstomial, evenly and numerously perforated.

Remarks. Before Osburn's sweeping revision of the family Smittinidae (1952 : 390–440), almost all Tertiary Smittinids were placed in either *Smittina* or *Porella*, both of which had become ungainly (see Lagaaij 1952 : 97, for a discussion of the nomenclatorial difficulties attending these genera). *Smittina*, as now restricted, includes species having an evenly perforated frontal, a median sub-oral avicularium, the orifice with lyrula and condyles, and an evenly perforated ovicell. Revision of the Eocene and Oligocene species which have in the past been assigned to *Smittina* and *Porella* will be a major undertaking. The list of species assignable to *Smittoidea* may be started with the following : *Smittia variabilis* Canu (described below) from the Eocene of England, Belgium, and France ; *Smittina angulata* (Münster) (Dartevelle 1952 : 191) from the Oligocene of Germany ; *Smittina orbavicularia* Canu & Bassler (1920: 469, pl. 61, figs. 1–4) from the Eocene of the Gulf Coast of the U.S.A. ; and *Smittina telum* Canu & Bassler (1920 : 468, pl. 93, figs. 1–9) and *Smittina reticuloides* Canu & Bassler (1920 : 467, pl. 96, figs. 1–9) from the Oligocene of the Gulf Coast, U.S.A.

Smittoidea variabilis (Canu)

(Text-figs. 42–47)

1908 *Smittia* (*Porella*) *variabilis* Canu : 97, pl. 8, figs. 1–7.
1929*a* *Smittina variabilis* (Canu) Canu & Bassler : 40.
1933 *Smittina variabilis* (Canu) ; Dartevelle : 107.
?1933 *Palmicellaria lerichei* Dartevelle : 82, pl. 3, figs. 3, 4.
1934 *Smittina variabilis* (Canu) ; Davis : 223, pl. 15, fig. 54.
1937 *Smittina variabilis* (Canu) ; Dartevelle : 110.
1946 *Smittina variabilis* (Canu) ; Buge : 435.
1949 *Porella variabilis* (Canu) Balavoine : 774.
1956 *Smittina variabilis* (Canu) ; Balavoine : 322.
1957 *Smittina variabilis* (Canu) ; Balavoine : 192.
?1963 *Trigonopora monilifera* (Milne Edwards) ; Malecki : 130, pl. 14, fig. 1 [*non Eschara monilifera* Milne Edwards].

Figured specimens. D.48676 (Text-fig. 42), D.48677 (Text-fig. 43), D.48678 (Text-fig. 44), D.48679 (Text-fig. 45), D.48679 (Text-figs. 46, 47).

Additional material. Forty-eight specimens, D.48680–D.48727.

Diagnosis. Encrusting or erect, uni- or bilaminar *Smittoidea* with zooecia extremely variable in size and form depending on zoarial type ; on encrusting portions, zooecia short, with thick, smooth frontals, well-developed peristomes, and large sub-oral avicularium on protuberant umbo ; on erect portions, zooecia longer, with

thinner, coarsely tuberculate frontals, short peristomes, and smaller avicularia or none ; orifice large, semi-circular, with stout condyles and a rudimentary lyrula ; oral spines lacking ; ovicell very wide and finely perforate.

Description. *Zoarium* encrusting, unilaminar, rising in uni- or bilaminar, erect fronds, the zooecia crudely aligned in longitudinal rows on unilaminar portions, regularly aligned in alternating series on bilaminar.

Zooecia on unilaminar portions irregularly hexagonal, pentagonal, or tetragonal, separated by narrow, salient threads. Length nearly one and a half times width. Frontal wall very convex and thick, highest at sub-oral umbo. Surface smooth, almost hyaline, with 3–4 large areolae in a single row on each proximo-lateral margin. Interareolar costules feebly developed, peripheral. Sub-oral umbo large, salient, massive. *Orifice* deeply buried in peristome, large, semi-circular, the distal margin evenly rounded, the proximal margin slightly convex, forming an incipient lyrula. Condyles paired, stout, placed on lateral margins close to proximal lip. Peristome irregular, forming a pair of high, lateral lappets, coalescing with the umbo, and a lower distal collar. Secondary orifice variable in shape depending on relative development of umbo, lappets, and avicularium.

Zooecia on bilaminar portions rectangular to rhomboidal, separated by narrow, raised threads. Length more than twice width. Frontal wall moderately convex and thick, highest near centre, except where avicularium is present. Surface smooth and almost hyaline at first but becoming coarsely tuberculate and porcellanous as calcification progresses. Areolae 5–7 along each proximo-lateral margin, without costules. Sub-oral umbo lacking, the avicularium, where present, occupying a swollen chamber covering most of the frontal surface. *Orifice* shallow, sub-terminal on frontal surface, large, semi-circular, the distal margin evenly rounded, the proximal margin convex, with a well-developed, broad, tapering, median lyrula. Condyles rudimentary. Peristome very short and thin, without distinct lateral lappets.

Avicularium adventitious, usually lacking on bilaminar fronds, single, median, sub-oral, placed on umbo or in swollen frontal chamber, usually facing into peristome, but with rostrum directed frontally and proximally. Rostrum rounded ; pivotal bar complete.

Ovicell hyperstomial, large, globular, wider than long, present on both uni- and bilaminar portions of zoarium. Surface evenly perforated with very small pores. Distal and lateral margins distinctly rimmed. Proximal margin obscured by elongated and inwardly bent peristomial lappets.

Measurements :

Zooecia on unilaminar portions

Lz (10) 0·447 (0·0661) mm., 0·31–0·56 mm.
lz (10) 0·325 (0·0397) mm., 0·23–0·36 mm.
ho (10) 0·120 (0·0121) mm., 0·10–0·14 mm.
lo (10) 0·146 (0·0130) mm., 0·13–0·17 mm.
Lav (5) 0·109 (0·0185) mm., 0·09–0·13 mm.
Lov (3) 0·239 (0·0171) mm., 0·22–0·26 mm.

Zooecia on bilaminar portions

Lz (10) 0·634 (0·1055) mm., 0·48–0·88 mm.
lz (10) 0·288 (0·0586) mm., 0·25–0·44 mm.
ho (10) 0·122 (0·0110) mm., 0·09–0·13 mm.
lo (10) 0·143 (0·0107) mm., 0·13–0·16 mm.
Lav (2) 0·111 (0·0121) mm., 0·10–0·12 mm.
Lov (4) 0·177 (0·0146) mm., 0·16–0·20 mm.

Remarks. There is so much difference in the appearance of the zooecia on the uni- and bilaminar fragments that they might easily be mistaken for distinct species. As in the Lower Bracklesham Beds (Davis 1934 : 223), unilaminar fragments account for the majority of Upper Bracklesham specimens.

Although the illustrations of *Palmicellaria lerichei* Dartevelle (1933 : pl. 3, figs. 3, 4) are not completely clear, they resemble the general aspect of bilaminar fragments of *S. variabilis*.

The bilaminar fragment described and illustrated by Malecki (1963 : 130, pl. 14, fig. 1) as *Trigonopora monilifera* is almost certainly referable to *S. variabilis*. The globular hyperstomial ovicell (described as entozooecial), the deeply notched peristome, and the median sub-oral avicularium are evident on the figure. Specimens from the Eocene of Rumania (supplied by Dr. Sten Schager) are identifiable with this species and similar to the one illustrated by Malecki.

Distribution. Eocene (Lutetian) ; England, Belgium, France. Eocene (Auversian) ; Belgium. Eocene (Ludian) ; Rumania, ?Poland.

Family **ESCHARELLIDAE** Levinsen

Genus ***ESCHARELLA*** Gray

Escharella selseyensis sp. nov.

(Text-figs. 48–50)

1908 *Smittia* (*Mucronella*) *hoernesi* (Reuss) ; Canu : 96, pl. 7, fig. 16.
1946 *Mucronella angustoecium* Gregory ; Buge : 435.

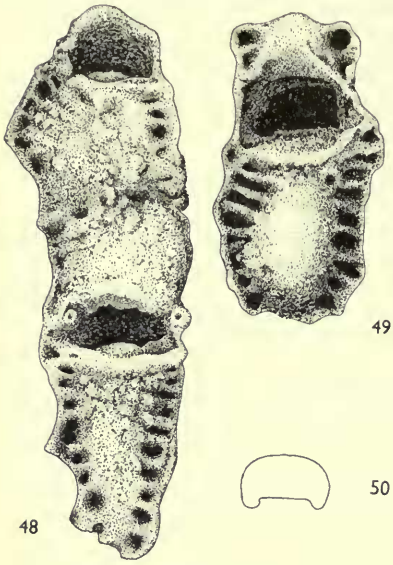
Holotype. D.48728 (Text-fig. 48).

Paratypes. D.48729 (Text-figs. 49, 50), D.48730, and L.S.U. 8035.

Diagnosis. Unilaminar, probably encrusting *Escharella* with broad lyrula in primary orifice and peristome raised proximally to form a broad, lip-like mucro ; distal margin of orifice with 2 small, evanescent spines ; ovicell large, globular.

Description. *Zoarium* unilaminar, presumably encrusting, with zooecia arranged in regular longitudinal rows, those in adjacent rows alternating in position.

Zooecia elongate oval, more broadly rounded distally than proximally, separated by a narrow, raised thread. Length nearly twice width. Frontal wall moderately thick, strongly convex, highest near centre. Frontal surface coarsely granular, sometimes with a large, protruding umbo covering the greater part. Areolae large,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elliptical, in a single, evenly spaced row of 16–20 on lateral and proximal margins. Inter-areolar costules short, thin, peripheral.

Orifice steeply inclined distally, deeply buried in peristome, semi-elliptical, with long axis transverse, the distal margin broadly rounded, the proximal margin straight or convex, with a broad, saddle-shaped, median lyrula. Peristome thin, granular, especially raised proximally to form a broad, lip-like mucro. Secondary orifice elliptical, with major axis transverse. Distal spines 2, small, evanescent.

Ovicell hyperstomial, globular; distal margin evenly rounded, marked by an irregular row of small areolae; proximal margin with a slightly thickened, arcuate rim. Surface coarsely granular, impunctate.

Heterozooecia lacking.

MEASUREMENTS:

Lz (8) 0·491 (0·0754) mm., 0·35–0·59 mm.
lz (5) 0·274 (0·0337) mm., 0·22–0·31 mm.
ho (6) 0·081 (0·0105) mm., 0·07–0·09 mm.
lo (5) 0·152 (0·0072) mm., 0·14–0·16 mm.
Lov (5) 0·219 (0·0130) mm., 0·20–0·24 mm.

REMARKS. The synonymy given by Canu (1908 : 96; 1913 : 149) for *Lepralia hoernesi* Reuss was considered to be heterogeneous by Canu & Bassler (1929*a* : 45). Canu's (1914*b*) Stampian material is probably conspecific with Reuss's (1865) Oligocene specimens, and both are probably referable to *Perigastrella*. Canu's (1908) Lutetian material is identifiable with the Upper Bracklesham specimens for which the name *Escharella selseyensis* is here proposed. *Mucronella angustoecium* Gregory, the Bartonian species (holotype, 49739, Edwards Collection, Barton, Hants) placed in synonymy by Canu (1908 : 96), differs from *E. selseyensis* in having larger zooecia with smaller, sub-circular orifices, and smaller ovicells.

DISTRIBUTION. Eocene (Lutetian); France.

Family **SERTELLIDAE** Jullien

Genus ***SERTELLA*** Jullien

Sertella marginata (Reuss)

(Text-figs. 51–53)

1865 *Retepora marginata* Reuss : 661, pl. 10, figs. 6, 7.
?1866 *Retepora marginata* Reuss; Reuss : 190.

FIGS. 48–53. Fig. 48. *Escharella selseyensis* sp. nov. D.48728. Holotype. Two zooecia, the proximal one ovicelled. Figs. 49, 50. *Escharella selseyensis* sp. nov. D.48729. Paratype. Zooecium with well-developed frontal umbo, and oral outline of another zooecium. Fig. 51. *Sertella marginata* (Reuss). D.48731. Dorsal aspect of a fragmentary zoarium. An avicularium occurs just over the fenestrule. Fig. 52. *Sertella marginata* (Reuss). D.48732. Ovicelled zooecium. Fig. 53. *Sertella marginata* (Reuss). D.48733. Part of a zoarial fragment showing zooecia with oral and frontal avicularia and several with fenestral ones as well.

FIGURED SPECIMENS. D.48731 (Text-fig. 51), D.48732 (Text-fig. 52), D.48733 (Text-fig. 53).

ADDITIONAL MATERIAL. Six specimens, D.48734–D.48739.

DIAGNOSIS. *Sertella* with triserial trabeculae of about same width as the elliptical fenestrules; zooecia frontally marginate with non-denticulate primary orifice and sinuate secondary orifice; oral avicularium mucronate; frontal avicularia rounded; fenestral avicularium pointed; dorsal avicularia spatulate.

DESCRIPTION. *Zoarium* erect, unilaminar, reticulated, the fenestrules elliptical, quincuncially arranged, of about same width as branches. Zooecia disposed in 3 longitudinal rows on frontal face of branch (trabecula), those in adjacent rows alternating in position. Dorsal face finely tuberculate, divided into large, irregular polygons by narrow, slightly raised threads (vibices).

Zooecia irregularly polygonal, separated by thick, low threads connecting orifices of adjoining rows. Zooecial length about one and a half times width. Frontal wall very thick, slightly convex. Surface smooth, imperforate.

Orifice deeply buried in peristome, not visible in frontal aspect, small, elliptical, with long axis transverse and proximal lip straight. No condyles or denticles present. Peristome very long but almost completely immersed in thick frontal wall. Secondary orifice pyriform, with wide, deep proximal notch. A small, evanescent spine base occurs at mid-length on each lateral margin.

Avicularia adventitious, frontal and dorsal, usually multiple and polymorphic: (1) *Oral*, single, of intermediate size, placed in proximal notch of secondary orifice, the rounded, non-mucronate rostrum projecting frontally; cross-bar complete. (2) *Ordinary-frontal*, single or paired, very small, placed on frontal wall, removed from orifice, rounded, without pivotal structure. (3) *Fenestral-frontal*, single, large, placed on frontal wall of zooecia in neighbourhood of fenestrules, the pointed rostrum directed transversely outwards; cross-bar complete. (4) *Dorsal*, large, widely scattered, the spatulate rostrum oriented more or less transversely to the axis of the trabecula; cross-bar complete.

Ovicell hyperstomial, elongate, globular, but flattened proximally. Surface smooth, with longitudinal fissure extending nearly whole length, narrow, often fusiform, the greatest width at mid-length or slightly distal to it.

MEASUREMENTS:

Length of fenestrule (6) 0·640 (0·1170) mm., 0·51–0·82 mm.
Width of fenestrule (6) 0·294 (0·0655) mm., 0·23–0·42 mm.
Lz (10) 0·307 (0·0195) mm., 0·27–0·32 mm.
lz (4) 0·175 (0·0110) mm., 0·16–0·19 mm.
ho (5) 0·056 (0·0098) mm., 0·04–0·07 mm. } secondary orifice
lo (6) 0·054 (0·0070) mm., 0·04–0·06 mm. } secondary orifice
Lov (6) 0·155 (0·0137) mm., 0·14–0·17 mm.
Lav (oral) (5) 0·051 (0·0105) mm., 0·04–0·07 mm.
Lav (frontal) (4) 0·030 (0·0049) mm., 0·02–0·03 mm.

Lav (fenestral) (3) 0·111 (0·0086) mm., 0·10–0·12 mm.
Lav (dorsal) (2) 0·115 (0·0181) mm., 0·10–0·13 mm.

Remarks. This species is very much like the type species of *Sertella*, *S. beaniana* (King), from which it differs primarily in having trabeculae and fenestrules of about the same width, secondary orifice with sinus, fenestral avicularia pointed rather than spatulate, and dorsal avicularia large and spatulate. Although Reuss's figures (1865, pl. 10, figs. 6, 7) are not completely clear, the Upper Bracklesham specimens seem to agree with them.

Distribution. Oligocene (Stampian); Germany. ?Miocene; Germany.

Family **SCHIZOPORELLIDAE** Jullien

Genus ***DAKARIA*** Jullien

1903 *Dakaria* Jullien *in* Jullien & Calvet : 90.

Type species (by original designation). *Dakaria chevreuxi* Jullien *in* Jullien & Calvet 1903 : 90, pl. 10, fig. 6. Recent; off Dakar, Senegal.

Diagnosis. Frontal wall calcareous, evenly perforated with numerous pores. Orifice with broad, rounded, proximal sinus. Avicularia lacking. Ovicells, if present, hidden from frontal view.

Remarks. This deceptively simple Schizoporellid genus is not yet completely understood. Harmer's (1957 : 1021) inclusion of *Watersipora* and *Cribella* in its synonymy is open to question.

Dakaria beyrichi (Stoliczka)

(Text-fig. 54)

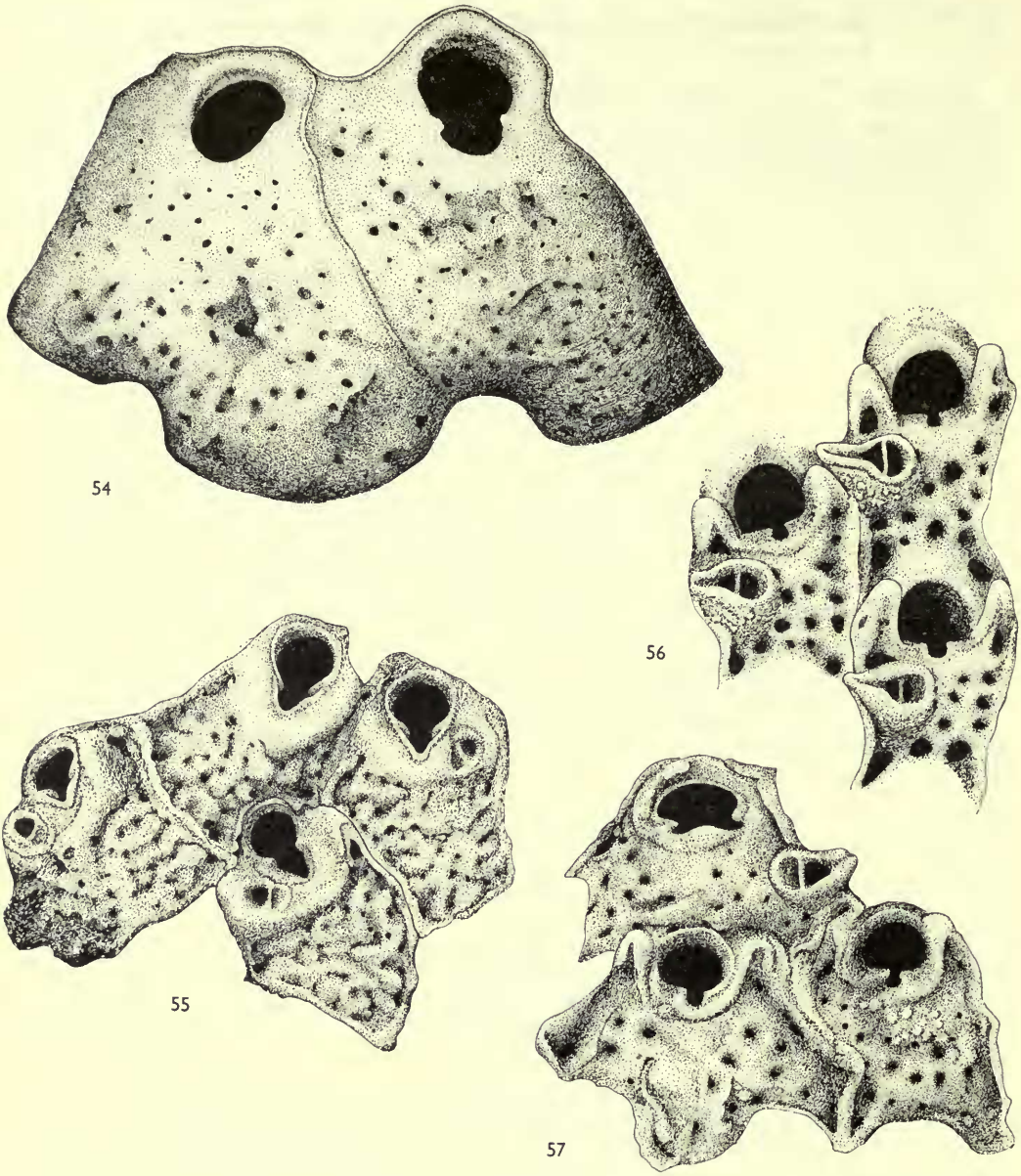
1862 *Cellaria beyrichi* Stoliczka : 83, pl. 1, fig. 10.
1908 *Hippoporina beyrichi* (Stoliczka) Canu : 83, pl. 6, fig. 2.
1935 *Dakaria beyrichi* (Stoliczka) Dartevelle : 115.
1946 *Hippoporina beyrichi* (Stoliczka); Buge : 434.
1952 *Dakaria beyrichi* (Stoliczka); Dartevelle : 190.
1956 *Dakaria beyrichi* (Stoliczka); Balavoine : 322.

Figured specimen. D.48740 (Text-fig. 54).

Diagnosis. Erect, cylindrical *Dakaria* with large, simple orifice lacking a peristome; ovicell unknown.

Description. *Zoarium* erect, cylindrical, the zooecia in 6–8 alternating, longitudinal rows.

Zooecia irregularly rhombic, separated by a faint groove at the crest of a wide, low thread. Zooecial length slightly less than width. Frontal wall moderately thick, very convex, highest near centre. Surface smooth, evenly perforated with numerous, small, circular, quincuncially arranged pores.



FIGS. 54–57. Fig. 54. *Dakari beyrichi* (Stoliczka). D.48740. Two zooecia. Fig. 55. *Schizomavella trigonostoma* sp. nov. D.48741. Holotype. Four zooecia, the one at upper left without an avicularium. Fig. 56. *Escharina procumbens* (Canu). D.48742. Three ovicelled zooecia from a unilaminar zoarial fragment. Fig. 57. *Escharina procumbens* (Canu). D.48743. Three non-ovicelled zooecia from a bilaminar fragment. The upper zooecium has the right margin of its orifice broken.

Orifice terminal on frontal surface, slightly inclined distally, the distal half slightly more than a semi-circle, the proximal sinus a slightly smaller semi-circle. Peristome, condyles lacking.

Heterozooecia lacking.

Ovicell unknown.

Measurements :

Lz (4) 0·635 (0·0409) mm., 0·59–0·68 mm.
lz (4) 0·667 (0·0908) mm., 0·56–0·77 mm.
ho (5) 0·180 (0·0337) mm., 0·13–0·22 mm.
lo (5) 0·161 (0·0112) mm., 0·14–0·17 mm.

Distribution. Eocene (Ypresian, Lutetian) ; France. Eocene (Lutetian) ; Belgium. Oligocene (Lattorfian) ; Germany.

Genus *SCHIZOMAVELLA* Canu & Bassler

?1893 *Schismoporella* Gregory : 243.
1917 *Schizomavella* Canu & Bassler : 40.
1917 *Metroperiella* Canu & Bassler : 40.

Type species (by original designation). *Lepralia auriculata* Hassall 1842 : 411. Recent ; British Isles.

Diagnosis. Frontal wall calcareous, evenly perforated with numerous pores. Orifice oval, with distinct median-proximal sinus between small condyles; sinus usually rounded and shallow. Peristome low, usually thin. Avicularium adventitious, single, frontal, proximal to orifice, directed longitudinally proximally or transversely, sometimes placed on a sub-oral umbo. Ovicell hyperstomial, globular, perforate.

Remarks. Harmer (1957 : 1024–1027) considered *Metroperiella* a distinct genus by virtue of its large ovicell surrounding the orifice of the ovicelled zooecium, but fossil species are intermediate between the two extremes. Buge (1953 : 322) regarded *Schismoporella* as a genus distinguishable from *Schizomavella* in having the avicularium removed from the orifice. Unfortunately, no such regularity of position as Buge implied characterizes these Schizoporellids (see e.g., Canu & Bassler 1920 : pl. 46, figs. 4–17 ; Brown 1952 : 235–238). Moreover, the type species of *Schismoporella*, *Lepralia schizogaster* Reuss (1848 : 84, pl. 10, fig. 9), requires re-study before its generic affinities can be definitely established. If it proves to be congeneric with *Schizomavella auriculata*, then *Schismoporella* will, of course, be the correct name of the genus.

Schizomavella trigonostoma sp. nov.

(Text-fig. 55)

Holotype. D.48741 (Text-fig. 55).

Paratype. L.S.U. 8036.

Diagnosis. Erect, bilaminar *Schizomavella* with rounded-trigonal orifice, the large, V-shaped sinus limited by stout lateral condyles; avicularium placed on proximo-lateral margin of orifice, the rostrum directed obliquely distally and outwards.

Description. *Zoarium* erect, bilaminar, compressed or cylindrical, the zooecia arranged in irregular longitudinal rows, those in adjacent rows alternating in position.

Zooecia irregularly rhomboidal, separated by a narrow, salient thread. Zooecial length slightly greater than width. Frontal wall moderately thick, slightly convex, highest near centre. Surface granular, evenly perforated with numerous, small, circular, quincuncially arranged pores.

Orifice entirely visible in frontal view, small, terminal on frontal wall, rounded trigonal, the distal margin evenly rounded, the proximal portion consisting of a very large, V-shaped sinus limited on each side by a stout, proximally directed condyle. Peristome thick but very low, widest proximally, smooth, flaring outwards.

Avicularium adventitious, single, frontal, placed on proximo-lateral margin of orifice, partly buried in peristome, with rostrum directed obliquely distally and outwards. Rostrum rounded. Pivotal bar complete.

Ovicell unknown.

Measurements:

Lz (5) 0·477 (0·0584) mm., 0·38–0·52 mm.
lz (5) 0·397 (0·1013) mm., 0·33–0·57 mm.
ho (6) 0·137 (0·0171) mm., 0·12–0·16 mm.
lo (6) 0·107 (0·0054) mm., 0·10–0·11 mm.
Lav (5) 0·128 (0·0191) mm., 0·10–0·15 mm.

Remarks. The orifice of this species, with a much longer sinus and stronger condyles than are typical of *Schizomavella*, finds a parallel in *S. dubia* Brown (1952 : 235, text-figs. 168, 169) from the Pliocene of New Zealand. The avicularium of *S. trigonostoma*, also atypical of *Schizomavella*, is similar in form, position, and orientation to that of *S. australis* (Haswell) (see Harmer 1957 : 1031, pl. 66, fig. 9).

Genus ***ESCHARINA*** Milne Edwards

Escharina procumbens (Canu)

(Text-figs. 56, 57)

1910 *Schizoporella hoernesi* var. *procumbens* Canu : 853, pl. 19, fig. 5.
1916 *Schizoporella hoernesi* (Reuss); Faura y Sans & Canu : 298.
1950 *Schizoporella hoernesi* (Reuss); Barroso : 179, text-fig. 7.

Figured specimens. D.48742 (Text-fig. 56), D.48743 (Text-fig. 57).

Diagnosis. Unilaminar or bilaminar, probably erect *Escharina* with somewhat elongate zooecia having coarsely perforate frontal and comparatively large orifice ; avicularium large, single, transversely and outwardly directed, with raised, swollen chamber ; a grooved, protuberant boss is developed from a frontal pore on each side of the orifice.

Description. *Zoarium* unilaminar, probably erect, tubular, sometimes becoming bilaminar, with zooecia arranged in longitudinal rows, those in adjacent rows alternating in position.

Zooecia irregularly rectangular to rhomboidal, separated by a narrow, raised thread. Length nearly one and a half times width. Frontal wall very slightly convex, moderately thick. Frontal surface finely tuberculate, perforated with large, evenly spaced pores, those along the margins tending to be larger.

Orifice large, semi-circular, completely visible in frontal view. Distal margin evenly rounded ; proximal margin nearly straight, interrupted medially by a narrow, shallow, rounded sinus. Peristome rudimentary. On each side of orifice occurs a tall, proximally grooved, protuberant boss originating from a frontal pore.

Avicularium adventitious, single or absent, large, frontal, placed on lateral margin at about mid-length, its rostrum transversely outwardly directed. Chamber slightly raised and swollen, the exterior tuberculate but imperforate. Rostrum channelled, pointed, produced slightly beyond border of zooecium. Pivotal bar complete.

Ovicell hyperstomial, recumbent, deeply immersed in distal zooecium, forming a small, hood-like swelling at distal margin of orifice. Surface imperforate, finely tuberculate, the proximal margin thickened, the distal margin merging with frontal wall of distal zooecium.

Measurements :

Lz	(7) 0·385 (0·0401) mm.,	0·32–0·43 mm.
lz	(7) 0·291 (0·0651) mm.,	0·23–0·38 mm.
ho	(7) 0·127 (0·0104) mm.,	0·11–0·14 mm.
lo	(8) 0·123 (0·0111) mm.,	0·10–0·11 mm.
Lav	(3) 0·154 (0·0171) mm.,	0·14–0·17 mm.
Lov	(2) 0·171 (0·0000) mm.,	0·17 mm.

Remarks. The Upper Bracklesham specimens agree best with the material from the Bartonian of Spain illustrated by Barroso (1950, text-fig. 7), from which they differ only in having well-developed lateral-oral bosses. The French specimens figured by Canu (1910 : pl. 19, fig. 5) have more numerous, smaller frontal pores and less-developed bosses. *E. hoernesi* (Reuss) has much more slender zooecia, smaller frontal pores, and much smaller avicularia in addition to lacking oral bosses entirely. Ovicells have not been noted heretofore in *E. procumbens*, though Reuss (1869*a* : pl. 33, figs. 6, 7) illustrated similar ones in *E. hoernesi*.

Distribution. Eocene (Lutetian, ?Auversian) ; France. Eocene (Lutetian, Bartonian) ; Spain.

Family **HIPPOPODINIDAE** Levinsen

Genus ***HIPPOPORINA*** Neviani

Hippoporina globulosa (d'Orbigny)

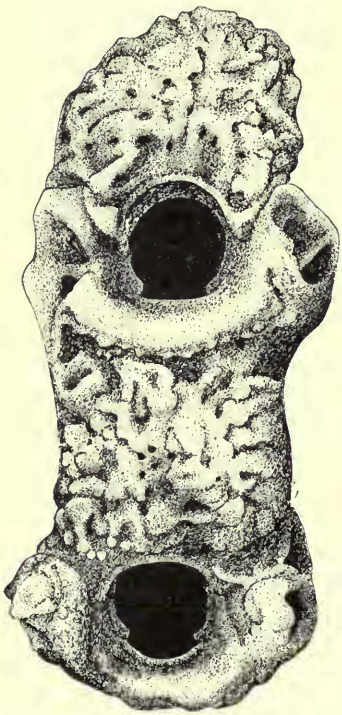
(Text-figs. 58, 59)

1851 *Reptescharellina globulosa* d'Orbigny : 453.
1908 *Hippoporina globulosa* (d'Orbigny) ; Canu : 82, pl. 6, fig. 9.
1933 *Hippoporina globulosa* (d'Orbigny) ; Dartevelle : 77.
1946 *Hippoporina globulosa* (d'Orbigny) ; Buge : 434.

FIGURED SPECIMENS. D.48744 (Text-fig. 58), D.48745 (Text-fig. 59).

DIAGNOSIS. Nodular, encrusting *Hippoporina* with paired, lateral-oral avicularia, the rostra directed inwards and distally ; ovicell large, globular, evenly perforated ; oral condyles stout, very close to proximal lip.

DESCRIPTION. *Zoarium* unilaminar, encrusting, forming irregularly globular masses, with the zooecia arranged in longitudinal rows, those in adjacent rows alternating in position.



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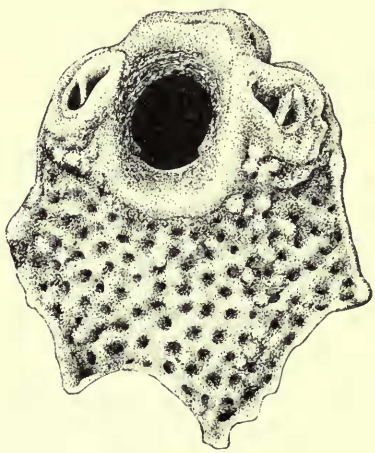

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0.500mm

FIGS. 58–59. Fig. 58. *Hippoporina globulosa* (d'Orbigny). D.48744. Two ovicelled zooecia, the proximal one incomplete. Fig. 59. *Hippoporina globulosa* (d'Orbigny). D.48745. Ordinary zooecium.

Zooecia irregularly rectangular, pentagonal, or rhomboidal, rounded distally, separated by narrow, sharp, raised threads. Zooecial length slightly greater than width. Frontal wall moderately thick, slightly convex, highest at proximal margin of peristome. Surface evenly perforated with numerous, closely spaced, quincuncially arranged, circular, funnel-shaped pores. Surface between pores ridged in a reticulate pattern, the intersections of the ridges often marked by small tubercles.

Orifice entirely visible in frontal view, large, elliptical, with major axis longitudinal, sub-terminal, slightly inclined distally. Condyles stout, paired, directed slightly proximally, placed on lateral margins very near proximal lip. Peristome thick but low, smooth, flaring outwards all round orifice, enclosing a very narrow, crescent-shaped bare spot proximally and occasionally distally as well.

Avicularia adventitious, frontal, paired, placed on lateral margins of peristome with rostra directed inwards and distally on to peristome. Rostrum pointed but not produced. Pivotal bar complete.

Ovicell hyperstomial, large, globular, deeply sunk in distal zooecium, but with proximal margin arching above orifice of ovicelled zooecium. Surface evenly perforated with numerous pores like those on frontal wall. Distal and proximal margins without rims. Orifice of ovicelled zooecia unmodified.

Measurements :

Lz (4) 0·646 (0·1037) mm., 0·56–0·77 mm.
lz (4) 0·517 (0·0649) mm., 0·45–0·61 mm.
ho (4) 0·156 (0·0108) mm., 0·14–0·17 mm.
lo (4) 0·162 (0·0070) mm., 0·15–0·17 mm.
Lav (3) 0·177 (0·0049) mm., 0·17–0·18 mm.
Lov (3) 0·399 (0·0131) mm., 0·38–0·41 mm.

Remarks. D'Orbigny (1851) did not illustrate his material; the holotype (Muséum national d'Histoire naturelle, Paris, no. 9648) was figured by Canu (1908 : pl. 6, fig. 9).

Distribution. Eocene (Lutetian, Auversian); France. Eocene (Auversian); Belgium.

Family **DITAXIPORINIDAE** Cheetham

Genus ***CABEROIDES*** Canu

1908 *Caberoides* Canu : 87.

Type species (by original designation). *Caberoides canaliculatus* Canu 1908 : 88, pl. 11, figs. 11, 12. Eocene (Lutetian); vicinity of Paris, France.

Diagnosis. Frontal wall calcareous, convex, irregularly perforated with scattered pores of variable size. Orifice terminal on frontal surface, broadly sinuate between small, widely spaced condyles proximally. Peristome thin, short. Interzooecial communication by simple pores. Vibracula adventitious, paired, with elongate chambers on frontal surface; additional oblique, slit-like vibracula sometimes present

on dorsal surface, following interzooecial sutures. Avicularium single, adventitious, placed on outer margin of zooecium, either above or below vibraculum, with short, pointed rostrum directed distally and outwards. Ovicell hyperstomial, elongate, globular, curved outwards from zooecial mid-line, ornamented with irregularly placed pores. Zoarium erect, jointed, branching at internodes ; internodes biserial, with orifices opening on one face only.

Remarks. Canu (1908 : 87) introduced this genus for two French Lutetian species, *C. canaliculatus*, the type, and *C. grignonensis* Canu (1908 : 88, pl. 11, figs. 14, 15), both of which display dorsal vibracula in addition to the frontal ones and have the frontal avicularium placed above the outer vibraculum. *C. corniculatus* sp. nov., described below, lacks dorsal vibracula and has the avicularium below the outer vibraculum.

The genus *Caberoides*, constituted of these three species, ranges from Lutetian to Auversian and is endemic to the Anglo–Paris Basin. I have earlier (Cheetham 1963*a* : 489) remarked upon the similarity of *Caberoides* and *Ditaxiporina* Stach and at that time erected the family Ditaxiporinidae for them.

Caberoides corniculatus sp. nov.

(Text-figs. 60, 61)

Holotype. D.48746 (Text-figs. 60, 61).

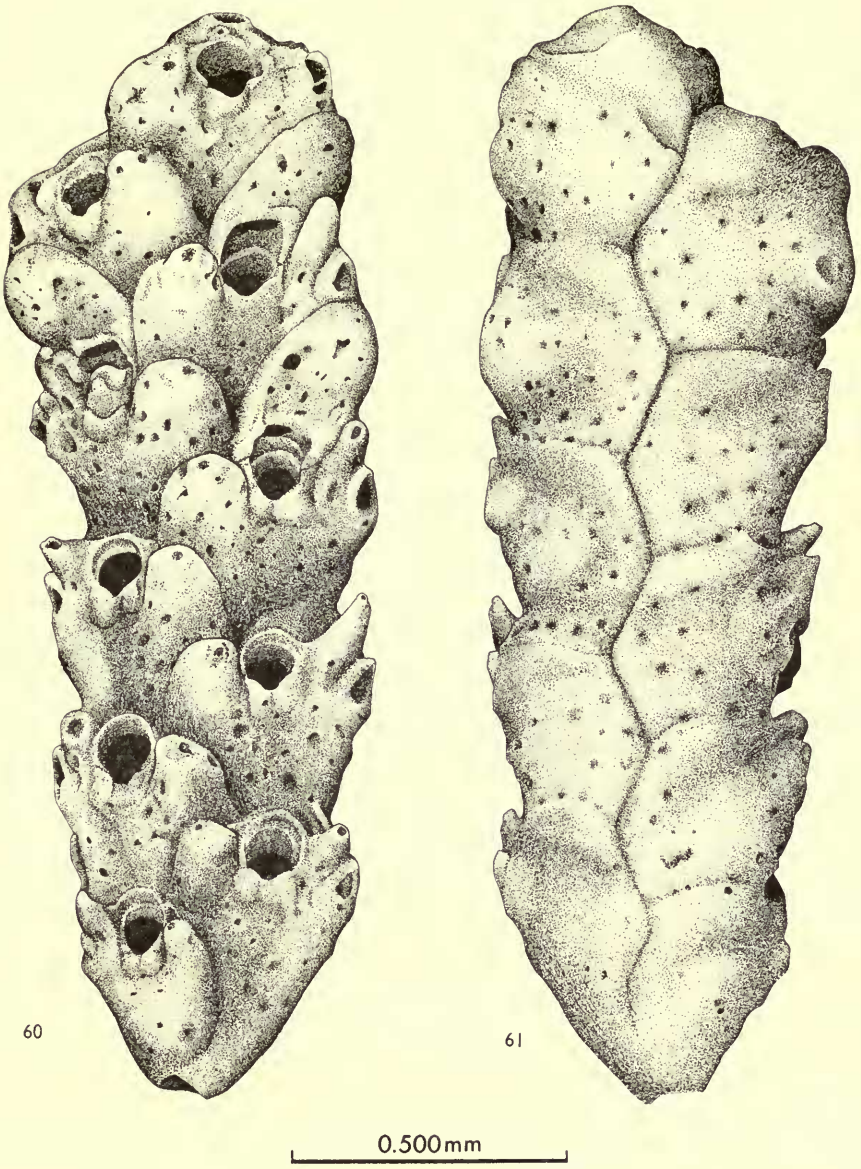
Paratypes. D.48747–D.48771 (25 specimens), and L.S.U. 8037.

Diagnosis. *Caberoides* with vibracula on frontal side only, paired, the outer one elongate and horn-like ; avicularium placed on chamber of outer vibraculum and below its opening ; ovicell curved outwards markedly, its surface with numerous, irregular perforations and 2–3 larger fenestrae.

Description. *Zoarium* erect, jointed, dichotomous at nodes. Internodes long, narrow, compressed, consisting of 10 or 12 zooecia arranged in 2 alternating series, with orifices all opening on one face. Proximal end of internode with single, simple, circular opening formed jointly by proximal ends of first zooecia of both series, one of which, either right or left, is slightly lower. Distal end of internode with 2 pores, one on mid-line of distal wall of last zooecium of each series.

Zooecia rhomboidal, distorted on frontal side by vibracular chambers, separated on both frontal and dorsal sides by grooves. Communication between zooecia of the same series by a single, median pore in distal wall ; between zooecia of adjacent series by simple pores along mid-line of inner lateral wall. Zooecial length slightly greater than width. Frontal wall thin, irregularly convex, highest at proximal lip of orifice. Frontal surface smooth, perforated irregularly by pores sometimes forming short tubules. Basal surface gently convex, perforated in same way as frontal.

Orifice terminal on frontal surface, large, inclined distally. Distal margin broadly and evenly rounded ; proximal margin broadly sinuate between a pair of small, widely spaced condyles. Peristome thin, short.



FIGS. 60, 61. *Caberoides corniculatus* sp. nov. D.48746. Holotype. Frontal and dorsal views of a nearly complete internode, showing 10 zooecia of which three are ovicelled.

Vibracula adventitious, paired, placed on lateral margins of frontal wall, opening beside orifice. Inner vibraculum with large, bulbous chamber, perforated like frontal wall on which it reposes, extending from proximal border of zooecium to orifice; distal margin of vibraculum with crescent-shaped slit. Inner vibracula of adjacent series form an irregular, zig-zag ridge down mid-line of internode face. Outer vibraculum with long, horn-like chamber projecting outwards from lateral margin of zooecium; vibracular slit straight, running down outer margin of chamber.

Avicularium adventitious, single, small, placed on chamber of outer vibraculum below its opening. Rostrum short, pointed, directed distally and slightly outwards. Opening divided by pivotal bar at least in some specimens.

Ovicell hyperstomial, elongate, globular, curved markedly outwards from longitudinal axis of zooecium, separated from distal zooecium by a furrow. Surface convex, smooth, perforated by irregularly spaced pores, 2–3 of which are commonly larger. Opening arched but very low, probably not closed by operculum, marked by a distinct ridge.

MEASUREMENTS:

Lz	(10) 0·349 (0·0224) mm.,	0·32–0·37 mm.
lz	(10) 0·321 (0·0340) mm.,	0·26–0·37 mm.
ho	(10) 0·091 (0·0092) mm.,	0·08–0·10 mm.
lo	(10) 0·098 (0·0073) mm.,	0·09–0·10 mm.
Lav	(10) 0·093 (0·0063) mm.,	0·09–0·10 mm.
Lov	(4) 0·297 (0·0043) mm.,	0·29–0·30 mm.

REMARKS. This species differs from both *C. canaliculatus* and *C. grignonensis*, not only in the position of the frontal avicularium and in lacking dorsal vibracula, but also in its more robust zooecia. Specimens of *C. canaliculatus* from the Sables de Fresville (Lutetian) at Gourbesville (Manche), France (supplied by Mr. Dennis Curry), are shorter (mean Lz = 0·30 mm. for 5 zooecia), and specimens of *C. grignonensis* from the same sample are narrower (mean lz = 0·26 mm. for 5 zooecia). The ovicells of the Gourbesville specimens do not show the characteristic ornamentation of the ovicell described by Canu (1908 : 88, 89), i.e. channelled in *C. canaliculatus* and carinate in *C. grignonensis*.

Family **TUBUCELLARIIDAE** Busk

Genus ***TUBUCELLA*** Canu & Bassler

1917 *Tubucella* Canu & Bassler : 62.

TYPE SPECIES (by original designation). *Eschara mamillaris* Milne Edwards 1836 : 336, pl. 11, fig. 10. Eocene (Lutetian); vicinity of Paris, France.

DIAGNOSIS. Frontal wall calcareous, inflated, perforated with evenly spaced, quincuncially arranged pores. Orifice small, semi-circular, hidden completely by a tubular peristome equal in length to the frontal wall. Ascopore not much larger than frontal pores, simple, single, placed on frontal wall near peristomial suture.

Scattered frontal avicularia present in some species. Ovicell peristomial, a small swelling near base of peristome of fertile zooecium ; fertile peristomes of different form from infertile ones. Zoarium erect, bilaminar, not jointed.

Remarks. This genus was established as a sub-genus of *Tubucellaria* d'Orbigny, but there is no tendency for the zoarium of *Tubucella* to be jointed, and avicularia, unknown in *Tubucellaria*, are present in many, though not the type, species of *Tubucella*.

Tubucella mamillaris (Milne Edwards)

(Text-figs. 62–64)

1836 *Eschara mamillaris* Milne Edwards : 336, pl. 11, fig. 10.
1907*a* *Tubucellaria mamillaris* (Milne Edwards) Canu : 515.
1908 *Tubucellaria mamillaris* (Milne Edwards) ; Canu : 78, pl. 6, figs. 3–6.
1910 *Tubucellaria mamillaris* (Milne Edwards) ; Canu : 848.
1917 *Tubucellaria* (*Tubucella*) *mamillaris* (Milne Edwards) ; Canu & Bassler : 62.
1918*a* *Tubucella mamillaris* (Milne Edwards) Canu : 358.
1925 *Tubucellaria mamillaris* (Milne Edwards) ; Canu : 47.
1929*a* *Tubucella mamillaris* (Milne Edwards) ; Canu & Bassler : 46.
1933 *Tubucellaria mamillaris* (Milne Edwards) ; Dartevelle : 102.
1935 *Tubucellaria mamillaris* (Milne Edwards) ; Dartevelle : 116.
1946 *Tubucellaria mamillaris* (Milne Edwards) ; Buge : 436.
1949 *Tubucella mamillaris* (Milne Edwards) ; Balavoine : 774.
1956 *Tubucella mamillaris* (Milne Edwards) ; Balavoine : 324.
1957 *Tubucella mamillaris* (Milne Edwards) ; Balavoine : 192.
1960 *Tubucella mamillaris* (Milne Edwards) ; Balavoine : 246.

Figured specimens. D.48772 (Text-fig. 62), D.48773 (Text-fig. 63), D.48774 (Text-fig. 64).

Additional material. Six specimens, D.48775–D.48780.

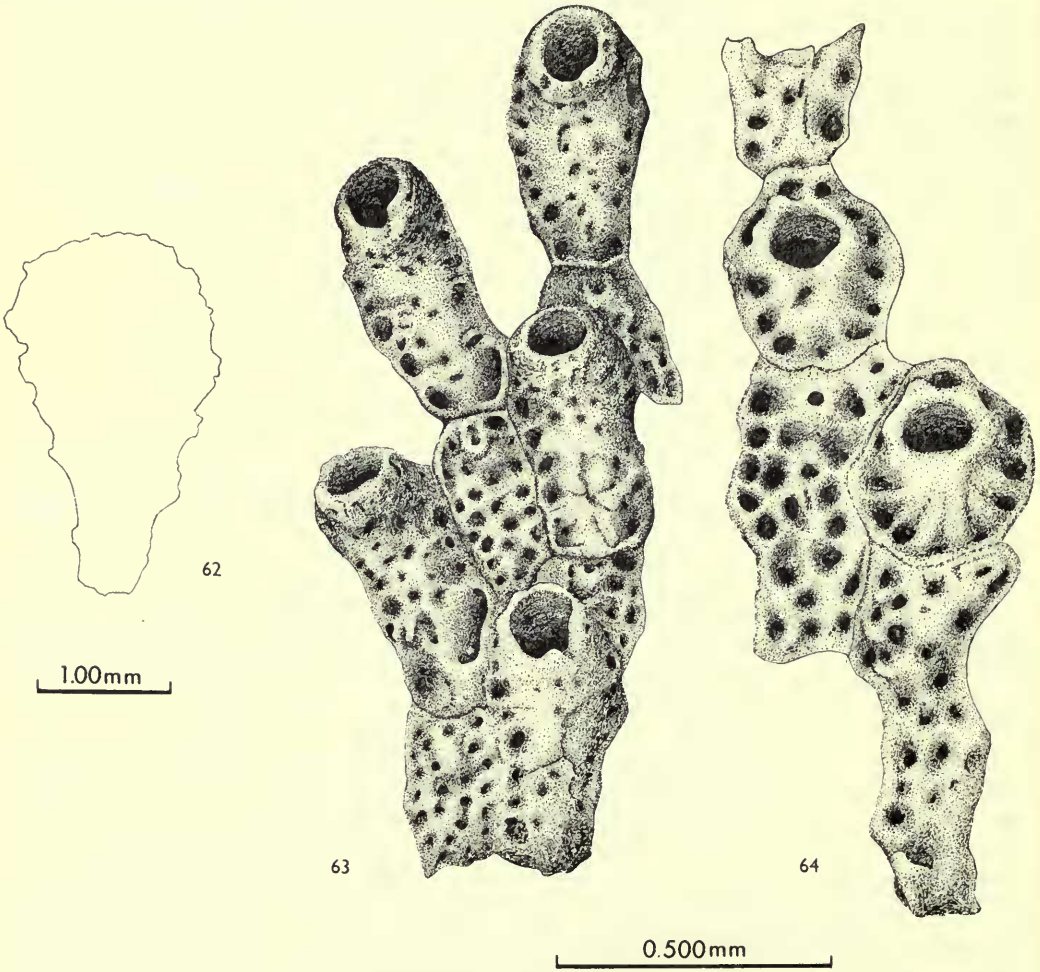
Diagnosis. *Tubucella* with most of the peristome pitted, sessile, and bordered by large pores, and with the free portion longitudinally costate ; ascopore on a small frontal prominence separated from peristome by a single row of pores ; fertile perstomes short, with a disto-lateral crown of pores ; avicularia lacking.

Description. *Zoarium* erect, bilaminar, cylindrical to compressed, typically forming lobate or flabellate branches originating as a cylinder of 6–8 rows of zooecia and widening into flattened fronds with 12–15 rows of zooecia on each side. Zooecia arranged in longitudinal rows, those in adjacent rows alternating in position.

Zooecia elongate, tubular, consisting of two regions of about equal length : a proximal frontal region bearing the ascopore, and a distal peristome bearing the secondary orifice. Zooecia separated by narrow, low threads. Frontal wall moderately thick, slightly convex, usually somewhat elevated immediately round the ascopore. Surface evenly perforated with large, circular, quincuncially arranged pores. Ascopore slightly larger than frontal pores, tilted distally, placed very near peristomial suture, with only a single row of frontal pores between.

Orifice small, semi-circular, with straight proximal lip, tilted distally, completely hidden from frontal view by peristome. Peristome sessile for most of its length, becoming free only at distal extremity. Sessile portion pitted and bordered on each side by a row of 5–8 circular pores, larger than the frontal pores. Free portion longitudinally costate or with longitudinal rows of small tubercles. Secondary orifice circular.

Ovicell small, peristomial, formed as a globular swelling in distal wall of peristome, near its base, hidden completely from frontal view. Ovicelled zooecia with frontal wall like that of non-ovicelled ones, but with much shorter and wider sessile peristome



FIGS. 62–64. Fig. 62. *Tubucella mamillaris* (Milne Edwards). D.48772. Outline of a zoarial fragment. Fig. 63. *Tubucella mamillaris* (Milne Edwards). D.48773. Five ordinary zooecia. Fig. 64. *Tubucella mamillaris* (Milne Edwards). D.48774. Two ovicelled zooecia and a small portion of a third, distal one.

bordered laterally and distally by a crown of 12 large pores. Free peristome short, longitudinally costate, with a slightly widened secondary orifice.

Avicularia lacking.

MEASUREMENTS :

Ordinary zooecia

Lz (7) 0·812 (0·0780) mm., 0·67–0·90 mm.
lz (7) 0·211 (0·0269) mm., 0·17–0·24 mm.
ho (7) 0·100 (0·0146) mm., 0·09–0·12 mm. } secondary orifice
lo (7) 0·106 (0·0190) mm., 0·09–0·13 mm. }
Length of peristome (7) 0·478 (0·0726) mm., 0·38–0·52 mm.

Ovicelled zooecia

ho (5) 0·099 (0·0076) mm., 0·09–0·11 mm. } secondary orifice
lo (5) 0·144 (0·0112) mm., 0·14–0·16 mm. }
Length of peristome (5) 0·333 (0·0200) mm., 0·30–0·35 mm.

DISTRIBUTION. Eocene (Lutetian, Auversian) ; France, Belgium. Oligocene (Stampian) ; France. Miocene (Aquitanian) ; France.

Family **ADEONIDAE** Hincks

Genus ***TEICHOPORA*** Gregory

1893 *Teichopora* Gregory : 249.
?1907*b* *Poristoma* Canu : 154.

TYPE SPECIES (by monotypy). *Teichopora clavata* Gregory 1893 : 249, pl. 31, figs. 5–7. Eocene (Bartonian) ; Barton Clay, Barton, Hampshire.

DIAGNOSIS. Frontal wall calcareous, smooth or granular, with single row of areolae continuing round distal margin. No ascopore or spiramen. Orifice sub-circular, with broad, U-shaped sinus proximally, without condyles. Peristome long enough to hide orifice, but immersed in thick frontal. Secondary orifice sub-circular, unmodified. Avicularia adventitious, small, single or paired, placed on proximo-lateral margins of orifice, becoming enclosed in thickening peristome so as to be nearly invisible exteriorly. Additional small, circular avicularia sometimes scattered over frontal. Gonoecia probably not of different form from zooecia. Zoarium erect, bilaminar, arborescent.

REMARKS. This genus has been poorly understood because its oral structure has never been clarified. Gregory (1893 : 249) described the orifice of the type species as simple and sub-circular, but he did not differentiate between the primary and secondary orifices. Actually, the orifices in the holotype (49733, Edwards Collection) are so filled with quartz grains that the structure of the primary orifice is completely obscured, but a paratype on the same slide, however poorly preserved in other respects, has a well-preserved orifice with a sinus but without condyles.

Canu & Caillot (1932 : 12), Canu (1926 : 456, 457), Davis (1934 : 228, 229), and Dartevelle (1933 : 108 ; 1936 : 29) all have confused *Teichopora* with *Bracebridgia*

MacGillivray. *Mucronella pyriformis* Busk, the Recent Indo-Pacific type species of *Bracebridgia* (lectotype, Department of Zoology, British Museum (Natural History), 87.12.9.615, Challenger Collection), differs from the European and British Eocene species in having a non-sinuate, semi-circular orifice with a short, broad lyrula occupying almost the entire proximal margin ; and vicarious, rather than adventitious avicularia. These differences are usually considered to be of generic magnitude in the Adeonidae ; therefore, the species exemplified by *T. clavata* and including at least *Eschara syringopora* Reuss in addition (see Waters 1891 : 20, pl. 3, figs. 2–4) must be excluded from *Bracebridgia*.

Canu (1907*b* : 154) introduced the genus *Poristoma* (consistently misspelt " *Porostoma* " in later works) for Adeonidae having " an avicularium developed in the peristomie or on the peristome " (translation). He listed under this generic name one *nomen nudum* (*Poristoma parisiensis*), one new species (*P. incisa*), and two species previously described (*T. clavata* Gregory and *Eschara polymorpha* Reuss). Selection of a type species for *Poristoma*, apparently an action that has not yet been taken, should be contingent upon a detailed study of *P. incisa* and *E. polymorpha*. Should *T. clavata* be chosen as type species, *Poristoma* would, of course, become an objective synonym of *Teichopora*.

Another genus which might be confused with *Teichopora* is *Meniscopora* Gregory, the type species of which, *M. bigibbera* Gregory (1893 : 251, pl. 31, figs. 8, 9 ; holotype 49732, Edwards Collection) from the Lower Bracklesham Beds, differs from *Teichopora* in having oral condyles and the avicularium always outside the peristome.

Teichopora clavata Gregory

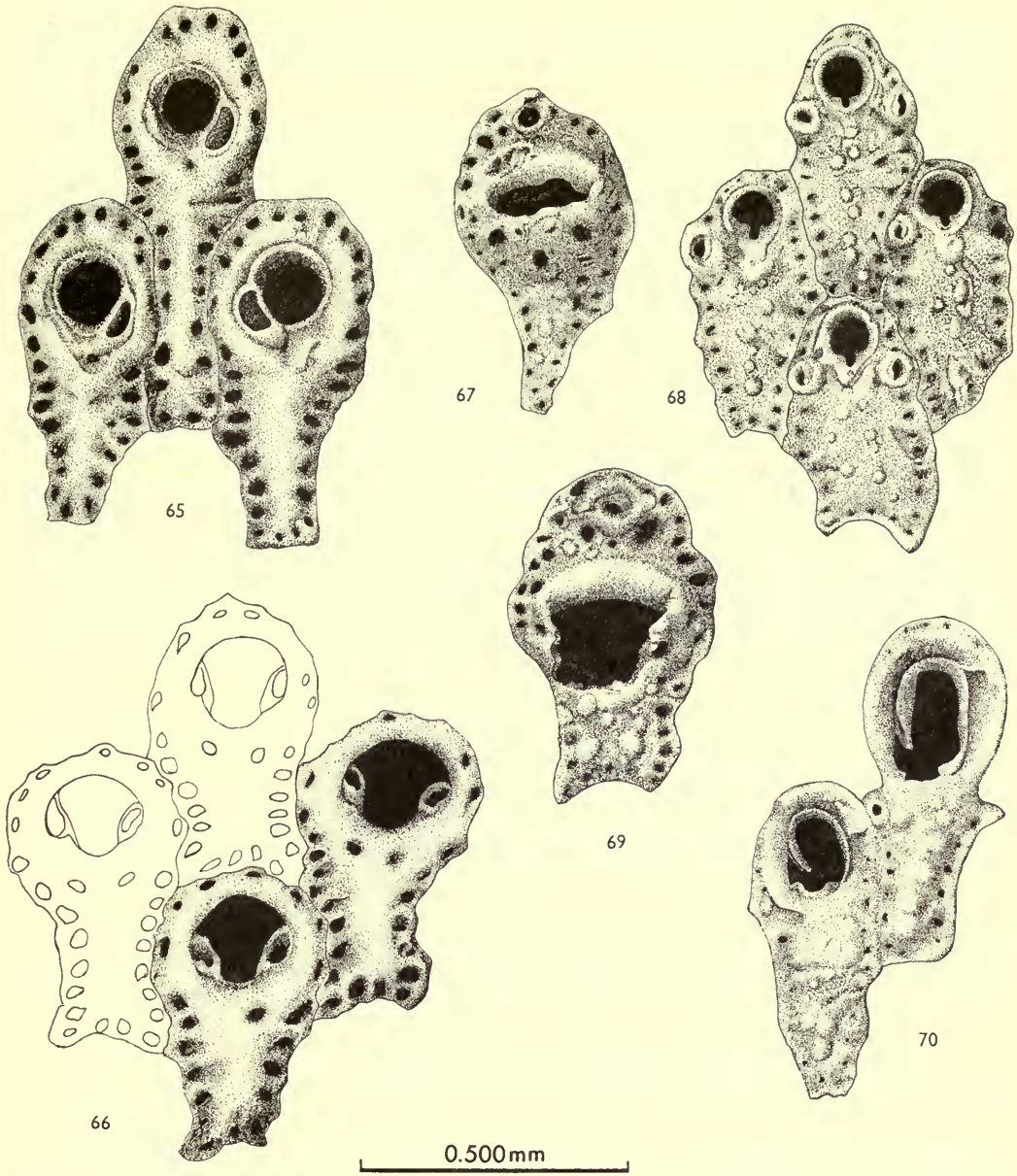
(Text-figs. 65, 66)

1893 *Teichopora clavata* Gregory : 249, pl. 31, figs. 5–7.
1907*b* *Poristoma clavata* (Gregory) Canu : 155, pl. 20, figs. 14, 15.
1925 *Bracebridgia clavata* (Gregory) Canu : 47.
1926 *Bracebridgia gyrinus* Canu : 756, pl. 28, figs. 3–6.
?1926 *Bracebridgia grandis* Canu : 757, pl. 28, figs. 1, 2.
1929 *Teichopora clavata* Gregory ; Burton : 328.
?1929*a* *Bracebridgia grandis* Canu ; Canu & Bassler : 49.
1933 *Bacebridgia* [sic] *gyrinus* Canu ; Dartevelle : 108.
?1933 *Bacebridgia* [sic] *grandis* Canu ; Dartevelle : 108.
1933 *Meniscopora clavata* (Gregory) Dartevelle : 114.
1936 *Bacebridgia* [sic] *gyrinus* Canu ; Dartevelle : 29.
?1936 *Bacebridgia* [sic] *grandis* Canu ; Dartevelle : 29.
1946 *Bracebridgia clavata* (Gregory) ; Buge : 436.

Holotype. 49733, Edwards Collection. Barton Clay ; Barton, Hants. Figured by Gregory (1893, pl. 31, fig. 5).

Figured specimens. D.48781 (Text-fig. 65), D.48782 (Text-fig. 66).

Additional material. Seventeen specimens, D.48783–D.48799.



FIGS. 65–70. Fig. 65. *Teichopora clavata* Gregory. D.48781. Three zooecia with single avicularium. Fig. 66. *Teichopora clavata* Gregory. D.48782. Four zooecia with paired avicularia. Fig. 67. *Schizostomella curryi* sp. nov. D.48800. Holotype. Nearly complete gonoecium. Fig. 68. *Schizostomella curryi* sp. nov. D.48801. Paratype. Four ordinary zooecia. Fig. 69. *Schizostomella curryi* sp. nov. D.48802. Paratype. Broken gonoecium. Fig. 70. *Schizostomella curryi* sp. nov. D.48803. Paratype. Two avicularian zooecia.

Diagnosis. *Teichopora* with the oral avicularia either single or paired, but never meeting across the secondary orifice, the rostrum directed distally and slightly outwards.

Description. *Zoarium* erect, arborescent, bilaminar, compressed, composed of longitudinal rows of zooecia, those in adjacent rows alternating in position.

Zooecia club-shaped, separated by very faint furrows. Length more than twice width. Frontal wall thick, strongly convex, with a prominent median longitudinal ridge connecting secondary orifice with proximal margin of zooecium. Frontal surface finely granular, with a single row of 20–30 large areolae evenly spaced round entire margin, and one or two additional pits just proximal to peristome on heavily calcified zooecia.

Orifice sub-circular to oval, the distal margin broadly rounded, the proximal margin curved to a slightly shorter radius to form a broad, median sinus. Peristome erect, not hiding distal areolae, very thick, long enough to hide orifice, but immersed in thickened frontal. Secondary orifice sub-circular, unmodified.

Avicularia adventitious, single or paired, placed on peristome at proximo-lateral margin of orifice, becoming enclosed by peristome as calcification advances. Rostrum rounded, directed distally and slightly outwards. Pivotal structure lacking.

Gonoecia, if present, not sufficiently differentiated from zooecia to be recognizable ; zooecia with paired avicularia and slightly enlarged secondary orifice may be gonoecia.

Measurements :

Zooecia with single avicularium

Lz	(5) 0·734 (0·0229) mm., 0·71–0·76 mm.	
lz	(5) 0·277 (0·0143) mm., 0·26–0·30 mm.	
ho	(5) 0·132 (0·0115) mm., 0·12–0·14 mm.	} secondary orifice
lo	(5) 0·126 (0·0153) mm., 0·11–0·14 mm.	} secondary orifice
Lav	(5) 0·106 (0·0130) mm., 0·09–0·13 mm.	

Zooecia with paired avicularia

Lz	(5) 0·530 (0·0264) mm., 0·50–0·54 mm.	
lz	(5) 0·311 (0·0155) mm., 0·29–0·33 mm.	
ho	(5) 0·156 (0·0127) mm., 0·14–0·17 mm.	} secondary orifice
lo	(5) 0·169 (0·0195) mm., 0·14–0·19 mm.	} secondary orifice
Lav	(5) 0·075 (0·0094) mm., 0·07–0·09 mm.	

Remarks. Canu (1926 : 757) separated the specimens from the French Auversian that he had previously identified with *T. clavata* and gave them the new name *B. grandis* because of their larger zooecia and orifices. At the same time he (1926 : 756) described *B. gyrinus* as a new species differing from *B. grandis* " only in its smaller dimensions and not regularly elliptical orifice " (translation). *B. gyrinus* thus appears to be a synonym of *T. clavata*, and *B. grandis* probably is also.

The holotype of *T. clavata* has its orifices filled with quartz grains, but the oral avicularium appears to be visible in one zooecium. The " gonoecia " described

and illustrated by Gregory (1893 : 249, pl. 31, fig. 6) in paratype 49757, Edwards Collection, seem to be frontally thickened ordinary zooecia from near the zoarial base.

T. syringopora (Reuss) differs from *T. clavata* principally in having the oral avicularia always paired and their rostra directed transversely inwards so that they frequently meet across the proximal part of the secondary orifice making a false ascopore (see Waters 1891 : pl. 3, figs. 2, 3).

Distribution. Eocene (Ypresian, Lutetian, Bartonian) ; France. Eocene (Auversian) ; England, ?Belgium. Eocene (Bartonian) ; England.

Genus ***SCHIZOSTOMELLA*** Canu & Bassler

1908 *Schizostoma* Canu : 69 (*non* Bronn 1834).
1927 *Schizostomella* Canu & Bassler : 20, 38.

Type species (by original designation). *Schizostoma crassum* Canu 1908 : 70, pl. 8, figs. 6–8. Eocene (Lutetian) ; vicinity of Paris, France.

Diagnosis. Frontal wall calcareous, finely granular to coarsely tuberculate or with large, irregular gibbosities. Areolae in one row or two, the outer one continuing round distal margin. Orifice oval, with distinct median-proximal sinus, deep and usually narrow, sometimes limited by small condyles. Peristome thick, becoming immersed in thickened frontal. Secondary orifice oval, without sinus. Avicularia adventitious, frontal, single or paired, placed on lateral margins of zooecium, usually near orifice, sometimes on distal portion of gonoecium. Rostrum rounded, cross-bar or condyles lacking. Vicarious avicularia, modified from ordinary zooecia by oral enlargement, present in some species. Gonoecia larger than zooecia, with wide, elliptical orifice, single or multiple ascopore (rarely lacking), and swollen distal portion with imperforate, marginally areolate surface.

Remarks. This characteristic British and European Tertiary genus has not yet been found in the New World. The following species, in addition to the type and *S. curryi* sp. nov. and *S. liancourti* (Canu) described below, seem to have been referred correctly to *Schizostomella* :

Schizostoma aviculiferum Canu (1908 : 71, pl. 8, fig. 12), Lutetian ; France.

Schizostoma denticulatum Canu (1908 : 72, pl. 7, figs. 14–16), Ypresian–Lutetian ; France.

Escharellina parnensis d'Orbigny (Canu 1908 : 74, pl. 8, figs. 14–16), Lutetian ; France.

Schizoporella magnoaperta Gregory (1893 : 239, pl. 33, fig. 9), London Clay ; Sheppey, Kent. Barton Beds ; Barton, Hants. Auversian ; France.

Eschara socialis Busk (Lagaaij 1952 : 120, pl. 13, figs. 4, 5, 7, 8), Coralline Crag ; Suffolk. Pliocene ; Holland.

Schizostoma gibbosum Canu (Buge 1957 : 296), Miocene and Pliocene ; France.

Schizostoma helveticum Canu & Lecointre (Buge 1957 : 297), Miocene and Pliocene ; France.

Eschara heteromorpha Reuss (Canu 1914*b* : 472, pl. 14, figs. 1–4, who erroneously referred it to *Metrarabdotos*), Oligocene ; France.

1. ***Schizostomella curryi***[11] sp. nov.

(Text-figs. 67–70)

Holotype. D.48800 (Text-fig. 67).

Paratypes. D.48801 (Text-fig. 68), D.48802 (Text-fig. 69), D.48803 (Text-fig. 70) ; D.48804–D.48905 (102 specimens) ; L.S.U. 8038.

Diagnosis. *Schizostomella* with relatively large zooecia having gibbosities and 24–28 areolae ; frontal avicularia usually paired, slightly removed from orifice ; vicarious avicularia little modified from zooecia ; gonoecia with a small distal avicularium and a single, median ascopore.

Description. *Zoarium* erect, arborescent, branching, composed of compressed, bilaminar fronds, with zooecia arranged in as many as 12 longitudinal rows, those in adjacent rows alternating in position. Number of zooecial rows increases distally by bifurcation. Base of zoarium small, encrusting.

Zooecia rhomboidal to club-shaped, very regularly arranged, not distorted round the gonoecia, separated by a faint groove. Communication between zooecia of the same series and adjacent series by simple pores placed in a single line of 14–16 near base of distal and disto-lateral walls. Zooecial length nearly twice width. Frontal surface finely granular, with larger gibbosities especially on central portion. Areolae small and circular proximally and laterally, smaller and slit-like distally, disposed in a single, evenly spaced row of 24–28 entirely round zooecial margin. Interareolar costules, where present, limited to periphery.

Orifice nearly terminal on frontal surface, small, not inclined to frontal plane. Distal portion semi-circular, with evenly rounded, smooth margin. Proximal portion straight, but interrupted medially in a deep, V-shaped or linear sinus. Peristome thin and short, never standing much above frontal surface nor obscuring primary orifice from frontal view. Secondary orifice oval, larger than primary one.

Avicularia dimorphic : small, adventitious and large, vicarious. Adventitious avicularia usually paired, rarely single or absent, placed on lateral corners of frontal wall over one or two areolae, having rounded rostra and lacking pivotal bar or condyles. Vicarious avicularia rare and sporadic, developed from zooecia by enlargement of orifice and oral region to greatly varying degrees. Avicularian orifice with broad distal shelf and greatly widened sinus flanked by small lateral condyles.

Gonoecia slightly longer and broader than ordinary zooecia, with small, paired, adventitious avicularia developed proximally and laterally to orifice and a third, small avicularium placed medially on distal margin. Gonoecial orifice a very wide

[11] After Mr. Dennis Curry.

ellipse separated from the single, rounded ascopore. Oral region strongly raised, the post-oral portion with a distal marginal crown of enlarged areolae, but not otherwise ornamented.

Measurements :

Ordinary zooecia

Lz	(10)	0·496 (0·0442) mm., 0·41–0·56 mm.
lz	(10)	0·239 (0·0171) mm., 0·21–0·26 mm.
ho	(10)	0·090 (0·0101) mm., 0·08–0·11 mm.
lo	(10)	0·088 (0·0107) mm., 0·08–0·11 mm.
Lav	(9)	0·070 (0·0153) mm., 0·05–0·09 mm.

Gonoecia

Lz	(5)	0·590 (0·0200) mm., 0·57–0·62 mm.
lz	(5)	0·332 (0·0398) mm., 0·27–0·38 mm.
ho	(4)	0·051 (0·0099) mm., 0·04–0·06 mm.
lo	(5)	0·188 (0·0326) mm., 0·17–0·21 mm.
Lav	(6)	0·067 (0·0219) mm., 0·05–0·10 mm.

Avicularian zooecia

Lz	(3)	0·616 (0·0342) mm., 0·58–0·65 mm.
lz	(3)	0·222 (0·0308) mm., 0·20–0·26 mm.
ho	(4)	0·165 (0·0214) mm., 0·14–0·19 mm.
lo	(4)	0·132 (0·0204) mm., 0·11–0·15 mm.

Remarks. The avicularian zooecia of this species are like the B-zooecia of *Steganoporella* in relation to the ordinary zooecia. It is, of course, possible that they represent a form of dimorphism different from avicularian, but the oral enlargement, markedly different from that of the gonoecia, is almost certainly a concomitant of opercular enlargement for presumably the same function as the development of avicularian mandibles.

S. curryi is very close to *S. gibbosa* (Canu), a French Miocene and Pliocene species, from which it differs in having avicularian zooecia and in having the gonoecia with a distal avicularium and a single, median ascopore.

2. ***Schizostomella liancourti*** (Canu)

(Text-figs. 71, 72)

1908 *Schizostoma liancourti* Canu : 72, pl. 22, figs. 10, 11.
1946 *Schizostomella liancourti* (Canu) Buge : 438.

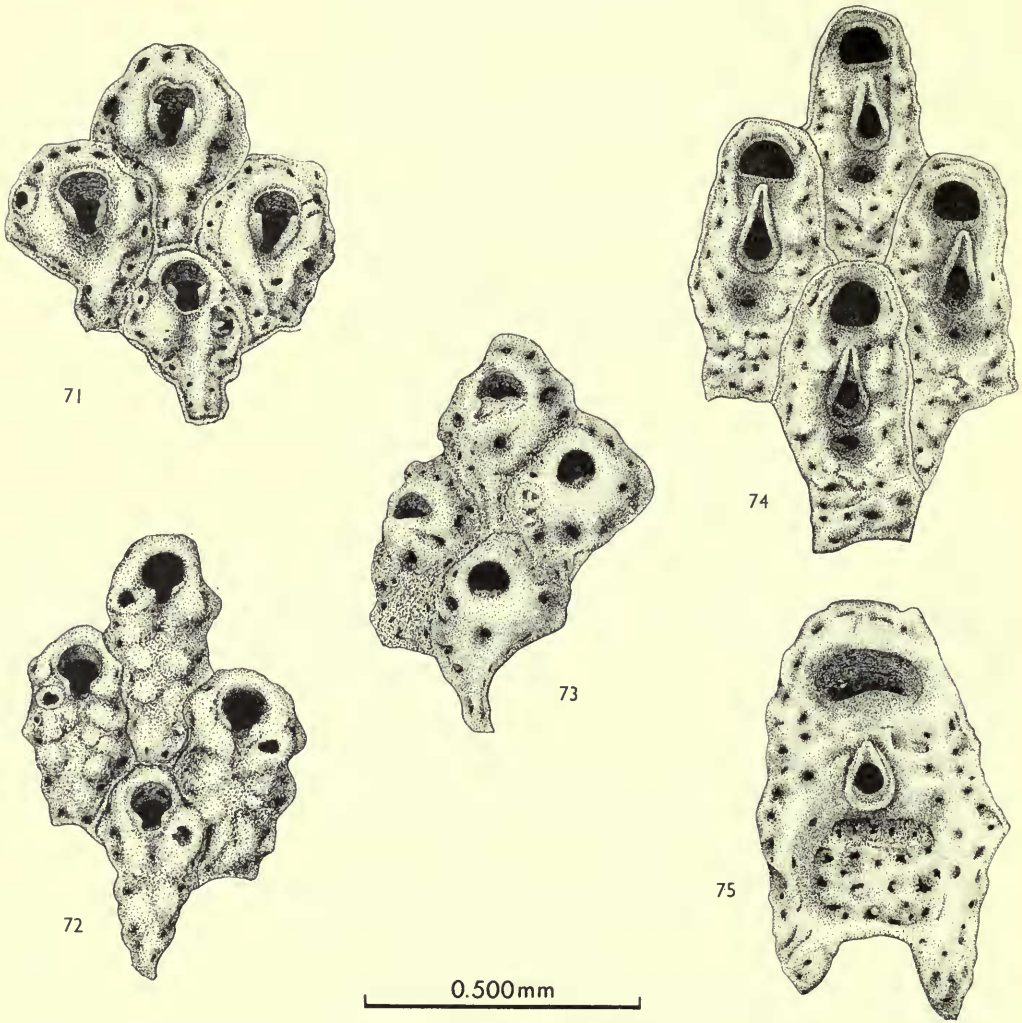
Figured specimens. D.48906 (Text-fig. 71), D.48907 (Text-fig. 72).

Additional material. Five specimens, D.48908–D.48912.

Diagnosis. *Schizostomella* with relatively small zooecia having tuberculate frontal walls with 14–20 areolae ; secondary orifice elongate, constricted at middle ;

frontal avicularia small, usually single, placed on peristome; vicarious avicularia lacking; gonoecium (*fide* Canu 1908 : 72) without distal avicularium or ascopore.

DESCRIPTION. *Zoarium* erect, arborescent, branching, composed of compressed, bilaminar fronds originating from a small, encrusting base. Zooecia arranged in 6–12 longitudinal rows on each side of frond, those in adjacent rows alternating in position.



FIGS. 71–75. Fig. 71. *Schizostomella liancourti* (Canu). D.48906. Four heavily calcified zooecia. Fig. 72. *Schizostomella liancourti* (Canu). D.48907. Four lightly calcified zooecia. Fig. 73. *Adeonellopsis selseyensis* sp. nov. D.48913. Holotype. Two gonoecia (on the left) and two zooecia. Fig. 74. *Adeonellopsis punctata* (Canu). D.48914. Four zooecia. Fig. 75. *Adeonellopsis punctata* (Canu). D.48915. Gonoecium.

Zooecia club-shaped, very regularly arranged, separated by a shallow groove. Communication between zooecia by simple pores. Zooecial length about one and a half times width. Frontal wall thick, convex, becoming flat with age, highest at proximo-lateral corners of orifice. Frontal surface tuberculate in thin-walled zooecia, becoming finely granular as wall thickens. Areolae small, circular, nearly occluding as calcification progresses, slit-like round distal margin, disposed in a single, evenly spaced row of 14–20 entirely round zooecial margin. Interareolar costules lacking.

Orifice sub-terminal on frontal surface, small, not inclined to frontal plane. Distal portion evenly rounded, smooth, semi-circular. Proximal portion nearly straight, interrupted medially in a deep but broad, U-shaped sinus. Peristome very thick, never standing much above frontal surface, but obscuring primary orifice from frontal view. Secondary orifice larger than primary one, constricted at middle so as nearly to form a spiramen.

Avicularia monomorphic, adventitious, usually single, rarely paired or multiple, placed on peristome near proximo-lateral corners of orifice, or on lateral margins of frontal wall, over one or two areolae. Rostrum rounded. Pivotal structures lacking.

Gonoecia lacking in material at hand.

MEASUREMENTS :

Lz	(10) 0·355 (0·0418) mm., 0·30–0·43 mm.		
lz	(10) 0·216 (0·0335) mm., 0·17–0·26 mm.		
ho	(9) 0·089 (0·0172) mm., 0·07–0·12 mm.	}	secondary orifice
lo	(11) 0·078 (0·0092) mm., 0·07–0·09 mm.	}	secondary orifice
Lav	(7) 0·077 (0·0131) mm., 0·05–0·09 mm.		

REMARKS. This species, hitherto known only from the French Lutetian, is easily distinguished from other species of *Schizostomella* by its constricted secondary orifice and its thick perstome on which the avicularia are placed. *S. crassa* (Canu) has a similar peristome, but its secondary orifice is different, and its frontal avicularium is well removed from the peristome. Canu (1908 : 72) characterized *S. liancourti* as always having paired or multiple avicularia, but his own illustrations (1908 : pl. 22, figs. 10, 11) show zooecia with single avicularium.

DISTRIBUTION. Eocene (Lutetian) ; France.

Genus ***ADEONELLOPSIS*** MacGillivray

Adeonellopsis selseyensis sp. nov.

(Text-fig. 73)

HOLOTYPE. D.48913 (Text-fig. 73).

DIAGNOSIS. *Adeonellopsis* with small, rhombic zooecia ; primary orifice visible in frontal aspect, proximal lip serrate ; ascopore simple or compound with as many as

5 perforations; avicularia frontal, paired lateral and occasionally single distal as well; gonoecia differ only slightly in size, shape, and oral structure from zooecia.

Description. *Zoarium* erect, arborescent, composed of compressed, bilaminar fronds with more than 7 longitudinal rows of zooecia on each side, the zooecia in adjacent rows alternating in position.

Zooecia rhombic, approximately equilateral, separated by distinct furrows. Length and width sub-equal. Frontal wall thick, markedly convex, highest round the proximal lip of the orifice. Frontal surface very finely granular, without tubercles or costules, margined by a single row of 18–20 small, circular areolae evenly spaced round the whole periphery. Ascopore placed just proximal to mid-length in a small, median pit, simple or compound, formed of a small circular disc with 2–5 minute perforations.

Orifice removed slightly from distal end of frontal surface, small, semi-circular, surrounded by a thick peristome, but not hidden from frontal view. Distal margin evenly rounded, smooth; proximal margin nearly straight, finely serrated. Peristome not elevated above frontal surface. Secondary orifice sub-circular.

Avicularia adventitious, frontal, small, multiple, their rostra rounded or slightly attenuated; pivotal structures lacking. One pair of avicularia present on each zooecium and gonoecium, one in each lateral corner; rostra directed inwards and slightly distally or proximally. An additional unpaired avicularium with rounded rostrum present on a few zooecia and gonoecia, placed on the distal part of the peristome, either on the mid-line or slightly to one side. Vicarious avicularia unknown.

Gonoecia slightly wider and longer than zooecia. Frontal wall like that of zooecia but more swollen round orifice. Ascopore, areolae, and avicularia similar to those of zooecia. Orifice slightly wider and shorter than that of zooecia, but with similar serration of proximal lip.

Measurements:

Zooecia

Lz	(5) 0·282 (0·0264) mm., 0·26–0·33 mm.	
lz	(5) 0·231 (0·0148) mm., 0·22–0·26 mm.	
ho	(5) 0·056 (0·0047) mm., 0·05–0·06 mm.	} secondary orifice
lo	(5) 0·067 (0·0038) mm., 0·06–0·07 mm.	} secondary orifice
Lav	(5) 0·044 (0·0038) mm., 0·04–0·05 mm.	

Gonoecia

Lz	(4) 0·355 (0·0110) mm., 0·34–0·38 mm.	
lz	(4) 0·250 (0·0214) mm., 0·22–0·27 mm.	
ho	(4) 0·043 (0·0000) mm., 0·04 mm.	} secondary orifice
lo	(4) 0·081 (0·0049) mm., 0·08–0·09 mm.	} secondary orifice
Lav	(4) 0·047 (0·0049) mm., 0·04–0·05 mm.	

Adeonellopsis punctata (Canu)

(Text-figs. 74, 75)

1907*b* *Adeonella punctata* Canu : 149, pl. 20, fig. 2.
1920 *Cribricella punctata* (Canu) Canu & Bassler : 564.
1946 *Adeonella punctata* Canu ; Buge : 436.
1960 *Adeonella punctata* Canu ; Balavoine : 246.
1963 " *Adeonellopsis punctata* (Reuss) " Malecki : 128, pl. 14, fig. 4.

FIGURED SPECIMENS. D.48914 (Text-fig. 74), D.48915 (Text-fig. 75).

ADDITIONAL MATERIAL. Forty-three specimens, D.48916–D.48959.

DIAGNOSIS. *Adeonellopsis* with large, rhomboidal zooecia ; primary orifice hidden from frontal view, the proximal lip smooth ; ascopore single and simple on zooecia, large and compound on gonoecia, with more than 20 perforations ; avicularium frontal, single, median, between orifice and ascopore, the rostrum directed distally ; gonoecia much larger than zooecia, the orifice greatly widened.

DESCRIPTION. *Zoarium* erect, arborescent, branching, composed of compressed, bilaminar fronds, originating from a small, encrusting base, expanding rapidly to as many as 20 longitudinal rows of zooecia on each side. Zooecia of adjoining rows alternate in position ; new rows added distally by intercalation.

Zooecia elongate, rhomboidal, variable in size and shape, but not distorted round gonoecia, separated by a furrow. Length nearly two-and-a-half times width. Frontal wall thick, only slightly convex, the area round the ascopore depressed. Surface finely granular, sometimes with small tubercles, margined entirely by a single, evenly spaced row of 20–30 small, circular areolae. Scattered areolae of a second, inner row sometimes present proximal to peristome and at proximal end of zooecium. Ascopore single, simple, circular, small, placed just proximal to mid-length in a very deep depression.

Orifice just short of distal end of zooecium, small, semi-circular, hidden by peristome from frontal view. Distal margin evenly rounded ; proximal margin nearly straight, smooth. Peristome thick, elongate, but generally buried in the frontal so that only distal and lateral portions are raised, sometimes enough to form a hood-like projection over orifice. Secondary orifice about same size and shape as primary one.

Avicularium adventitious, frontal, placed between orifice and ascopore, with rostrum directed distally, either longitudinally or slightly obliquely. Rounded end of avicularium stops short of ascopore-pit, and rostrum does not quite reach peristome. Rostrum raised, pointed, slightly channelled. Pivotal structure lacking.

Gonoecium slightly longer than and about twice as wide as zooecium. Frontal wall swollen all round orifice, with additional rows of areolae developed proximal to orifice. Ascopore greatly enlarged, compound, consisting of a flat, roughly circular disc perforated by 20 or more small pores. Orifice wider than that of zooecium, the proximal lip distinctly convex. Avicularium smaller than that of zooecium.

MEASUREMENTS :

Zooecia

Lz (10) 0·508 (0·0689) mm., 0·43–0·62 mm.
lz (10) 0·210 (0·0198) mm., 0·19–0·24 mm.
ho (10) 0·080 (0·0099) mm., 0·06–0·09 mm. } secondary orifice
lo (10) 0·091 (0·0070) mm., 0·09–0·10 mm. } secondary orifice
Lav (10) 0·160 (0·0285) mm., 0·13–0·22 mm.

Gonoecia

Lz (2) 0·573 (0·0363) mm., 0·55–0·60 mm.
lz (2) 0·423 (0·0665) mm., 0·38–0·47 mm.
ho (2) 0·077 (0·0121) mm., 0·07–0·09 mm. } secondary orifice
lo (2) 0·197 (0·0121) mm., 0·19–0·20 mm. } secondary orifice
Lav (2) 0·124 (0·0181) mm., 0·11–0·14 mm.

REMARKS. This species does not appear to be the same as the German Oligocene species reported by Reuss (1865 : 649, pl. 12, figs. 1, 2) as *Eschara coscinophora* Reuss and placed in synonymy with *A. punctata* by Canu (1907*b* : 149). *E. coscinophora* from the Miocene of Austria is conspecific with *E. imbricata* Philippi according to Lagaaij (1952 : 120). Therefore, the synonymy given by Malecki (1963 : 128) is too inclusive.

The generic assignment of *A. punctata* is difficult to make. The presence of an ascopore rather than a spiramen excludes it from *Adeonella* Busk (see Harmer 1957 : 802). Three genera of Adeonidae have well-developed ascopores : *Adeona* Lamouroux, *Adeonellopsis* MacGillivray, and *Reptadeonella* Busk. Harmer (1957 : 789–802, 814–818) differentiated these genera principally upon zoarial characters, at least some of which are not always evident in fragmentary fossil material. Cheetham & Sandberg (1964 : 1039) characterized *Reptadeonella* as having a simple, single or rarely double ascopore on both zooecia and gonoecia ; a sub-oral, median avicularium directed transversely or longitudinally or obliquely distally, its rostrum reaching the peristome ; occasionally additional frontal avicularia near the proximal margin of the zooecium ; and gonoecia with wide, short secondary orifice but not otherwise differentiated from the zooecia.

The type species of *Adeona*, *A. grisea* Lamouroux (chosen by Gregory 1893), represented in the Department of Zoology, British Museum (Natural History) by specimens such as 99.7.1.2750 and 2753, Busk Collection, has a simple, single or double ascopore on both zooecia and gonoecia ; a single, frontal avicularium flanking the ascopore distally and directed transversely or obliquely distally, its rostrum not reaching the peristome ; and gonoecia larger than the zooecia, with short, wide orifices.

Adeonellopsis seems to be much more variable than the other two ascopore-bearing Adeonid genera. The type species, *A. foliacea* MacGillivray (chosen by Canu & Bassler 1917), represented in the Department of Zoology, British Museum (Natural History) by specimen 97.5.1.709, has a compound ascopore on both zooecia and

gonoecia ; multiple sub-oral avicularia, both median and lateral, none with rostra reaching the peristome, on the zooecia ; supra-oral avicularia additionally on the gonoecia ; and gonoecia larger than the zooecia, with widened orifices.

Because of its compound gonoecial ascopore, *A. punctata* seems to fit best in *Adeonellopsis*, even though it has a single sub-oral avicularium and a simple zooecial ascopore. In these respects it resembles *Adeonellopsis arculifera* (Canu & Bassler) and *A. parvipuncta* MacGillivray (see Harmer 1957 : pl. 56, figs. 13, 14, 16).

Distribution. Eocene (Lutetian) ; France. Eocene (Ludian) ; Poland.

Family **CELLEPORINIDAE** Harmer

Genus ***CELLEPORINA*** Gray

Celleporina thomasi[12] sp. nov.

(Text-figs. 76, 77)

Holotype. D.48960 (Text-fig. 76).

Paratypes. D.48961 (Text-fig. 77) ; D.48962–D.48970 (9 specimens) ; L.S.U. 8039.

Diagnosis. *Celleporina* with median sub-oral avicularium on a prominent umbo and with lateral-oral bosses ; distal hood of ovicell forming a narrow rim within which is a row of small, marginal pores.

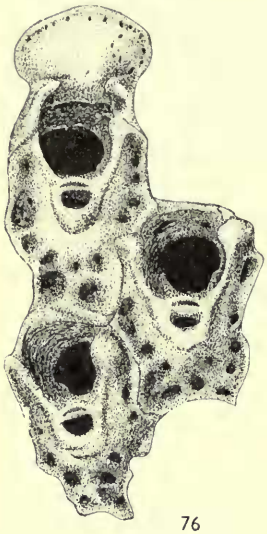
Description. *Zoarium* encrusting, unilaminar, the zooecia arranged in irregular longitudinal rows, those in adjacent rows alternating in position. Portions of zoaria probably rose as unilaminar tubes from the substrate.

Zooecia irregularly rhomboidal, separated by narrow, raised threads with a faint groove at the crest. Length almost twice width. Frontal wall thin, nearly flat except at sub-oral umbo. Surface tuberculate, radially striated, with large, circular areolae in a single marginal row of 4–6 on each side and usually an additional 2–3 proximally. Interareolar costules weak, peripheral. Sub-oral umbo, lacking on a few zooecia, usually massive.

Orifice commonly partly obscured in frontal view by proximal umbo and lateral bosses, oval, the distal portion semi-circular, the proximal portion a deep, wide, rounded sinus between a pair of rudimentary, widely spaced, lateral condyles. Peristome an irregular distal ridge, not differentiated from frontal surface, thick, smooth, terminating on each side of the orifice in a tubercle which enlarges to form a boss with advancing calcification, and which connects with the sub-oral umbo.

Avicularium adventitious, sometimes lacking, single, median, sub-oral, placed on the umbo, sometimes facing into the peristome, but with rostrum directed frontally, proximally, and usually slightly to one side. Rostrum rounded ; pivotal bar complete.

[12] After Dr. H. Dighton Thomas.



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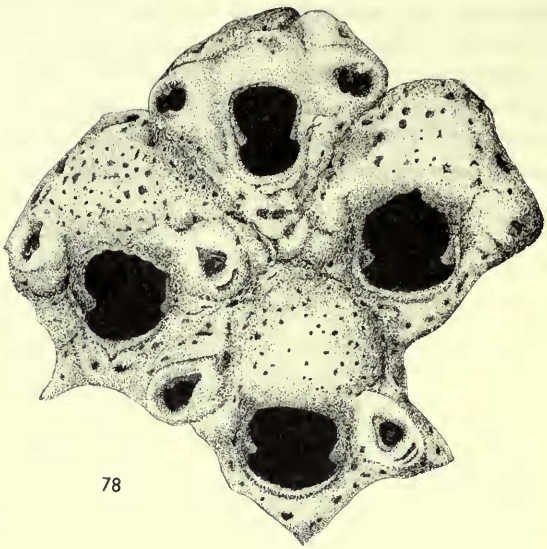

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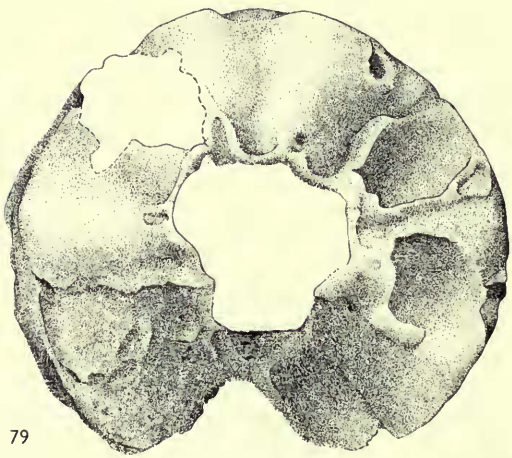

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1.00mm

FIGS. 76–79. Fig. 76. *Celleporina thomasi* sp. nov. D.48960. Holotype. Three heavily calcified zooecia, all with oral avicularia and one with an ovicell. Fig. 77. *Celleporina thomasi* sp. nov. D.48961. Paratype. Two lightly calcified zooecia lacking avicularia. Fig. 78. *Kionidella hastingsae* sp. nov. D.48971. Holotype. Four zooecia, three with ovicells. Fig. 79. *Kionidella hastingsae* sp. nov. D.48972. Paratype. Basal view of a hollow zoarial fragment.

Ovicell hyperstomial, globular, wider than long ; surface irregularly tuberculate, with a smooth, raised distal rim within which is a marginal row of small pores. Additional pores sometimes scattered over the surface. Proximal margin of ovicell generally visible between peristomial ridges which extend on to its surface.

Measurements :

Lz	(10) 0·397 (0·0513) mm.,	0·36–0·50 mm.
lz	(10) 0·221 (0·0224) mm.,	0·19–0·26 mm.
ho	(10) 0·115 (0·0157) mm.,	0·09–0·14 mm.
lo	(10) 0·101 (0·0054) mm.,	0·09–0·11 mm.
Lav	(10) 0·092 (0·0079) mm.,	0·09–0·10 mm.
Lov	(6) 0·167 (0·0105) mm.,	0·15–0·18 mm.

Remarks. This species, the oldest referred to *Celleporina*, differs from Recent species of the genus in having the ovicell with numerous pores and without the hood-like extension of the distal rim, and in having the frontal avicularium median sub-oral rather than lateral. The lateral oral bosses may foreshadow the lateral columnar avicularia so characteristic of later species. Otherwise the Upper Brackle-sham species fits well in *Celleporina*.

Family **MAMILLOPORIDAE** Canu & Bassler

Genus ***KIONIDELLA*** Koschinsky

1885 *Kionidella* Koschinsky : 67.

Type species (chosen by Canu & Bassler 1929*b*). *K. excelsa* Koschinsky 1885 : 68, pl. 7, figs. 5–12. Eocene (Lutetian) ; Bavaria.

Diagnosis. Frontal wall calcareous, smooth or granular, without pores or areolae. Orifice elongate, with lateral condyles and a thin, smooth peristome. Avicularia adventitious, single or paired, lacking on some zooecia, placed on lateral margins of frontal, with long or short rostrum directed inwards. Zooecia erect, prismatic, with just orifice and small area of frontal wall showing on frontal surface, communicating by simple pores placed low in zooecial walls. Zoarium hollow, tubular, unilaminar, ancestrular end closed, and distal ends of zooecia directed towards distal margin of zoarium. Ovicell hyperstomial, large, not raised above zoarial surface.

Remarks. The presence of ovicells in *Kionidella* was first noted by Waters in the type species (1891 : 29, pl. 4, fig. 6). Canu (*in* Buge 1946 : 438) later misinterpreted the ovicell as intermediate between entozooecial and entotoichal. Waters's figure indicates, and the specimens of *K. hastingsae* sp. nov. described below substantiate, that the ovicell of this genus is hyperstomial but deeply immersed, similar to that of *Mamillopora*.

Canu & Bassler (1929*b* : 477) placed *Kionidella* in synonymy with *Discoflustrellaria*, a genus founded by d'Orbigny (1853 : 508) for three species : *D. dactylus* d'Orbigny (1853 : 508, not figured) from the Lutetian of France ; *D. clypeiformis* d'Orbigny (1853 : 508, pl. 722, figs. 2–5) and *D. doma* d'Orbigny (1853 : 509, pl. 722, figs. 6–10),

both Lunulitidae from the Senonian of France. Canu (1900 : 378) indicated the type species of *Discoflustrellaria* to be *D. clypeiformis*, yet Canu & Bassler (1929*b* : 479) seem to have regarded *D. dactylus* as the type species when they stated, " D'Orbigny's name *Discoflustrellaria* is the older, but the French author did not give a single figure of the genotype. The latter was figured only in 1908 by Canu." This is presumably a reference to Canu (1908 : 103, pl. 9, fig. 18) who described and illustrated *D. dactylus* which Canu & Bassler (1929*b* : 478) referred to *Kionidella*. Thus Canu & Bassler seem to have been mistaken in considering *Kionidella* a synonym of *Discoflustrellaria*.

Kionidella hastingsae[13] sp. nov.

(Text-figs. 78, 79)

Holotype. D.48971 (Text-fig. 78).

Paratype. D.48972 (Text-fig. 79).

Diagnosis. *Kionidella* with zooecia wide and rhombic in frontal aspect, the frontal wall finely pitted ; oral condyles slightly proximal to mid-length, and sinus as broad as distal part of orifice ; avicularia paired, lateral, relatively small, and with pivotal bar ; rostrum rounded ; ovicells large, pitted, the fertile zooecia with widened orifice.

Description. *Zoarium* cylindrical, tubular, composed of a single layer of zooecia ; ancestrular end not preserved ; axial hollow circular in cross section, slightly larger in diameter than a zooecium. Zooecia in 14 very regular longitudinal rows round surface of cylinder.

Zooecia vase-shaped, their long axes perpendicular to zoarial axis, with only orifices and small part of frontal wall, of rhombic shape, exposed at outer surface. Frontal surfaces of adjoining zooecia separated by distinct grooves. Frontal wall imperforate, convex, finely pitted. Interzooecial communication by a few simple pores placed near base of distal and lateral walls.

Orifice elliptical, longer than wide, divided just proximal to middle by a pair of small, lateral, proximally inclined condyles, the sinus thus formed being as broad as the distal part of the orifice.

Avicularia adventitious, usually paired, placed in lateral corners of frontal surface just distal to middle of orifice. Avicularian opesia sub-circular, divided by a pivotal bar. Rostrum rounded, but somewhat elongated, directed inwards and slightly distally over orifice.

Ovicell hyperstomial, convex but not much raised above zoarial surface, semicircular, of about same length as zooecium. Surface finely pitted, imperforate. Orifice of fertile zooecia widened.

[13] After Dr. Anna B. Hastings.

MEASUREMENTS :

Ordinary zooecia

Lz (5) 0·349 (0·0693) mm., 0·26–0·44 mm.
lz (5) 0·383 (0·0237) mm., 0·34–0·39 mm.
ho (5) 0·157 (0·0097) mm., 0·14–0·17 mm.
lo (6) 0·117 (0·0100) mm., 0·10–0·13 mm.
Lav (6) 0·141 (0·0200) mm., 0·13–0·17 mm.

Ovicelled zooecia

lo (4) 0·180 (0·0070) mm., 0·17–0·19 mm.
Lov (5) 0·209 (0·0215) mm., 0·17–0·22 mm.

REMARKS. This species is most like *K. obliqueseriata* Koschinsky (1885 : 69, pl. 7, figs. 13*a*, *b*) from the Lutetian of Bavaria. The two species differ primarily in the form of the avicularium : in *K. obliqueseriata* it is single and has a long, pointed rostrum. *K. excelsa* Koschinsky and *K. dactylus* (d'Orbigny) differ from *K. hastingsae* in the form of the avicularium and also in the shape of the zooecia and orifice.

Family **ORBITULIPORIDAE** Canu & Bassler

Genus ***ORBITULIPORA*** Stoliczka

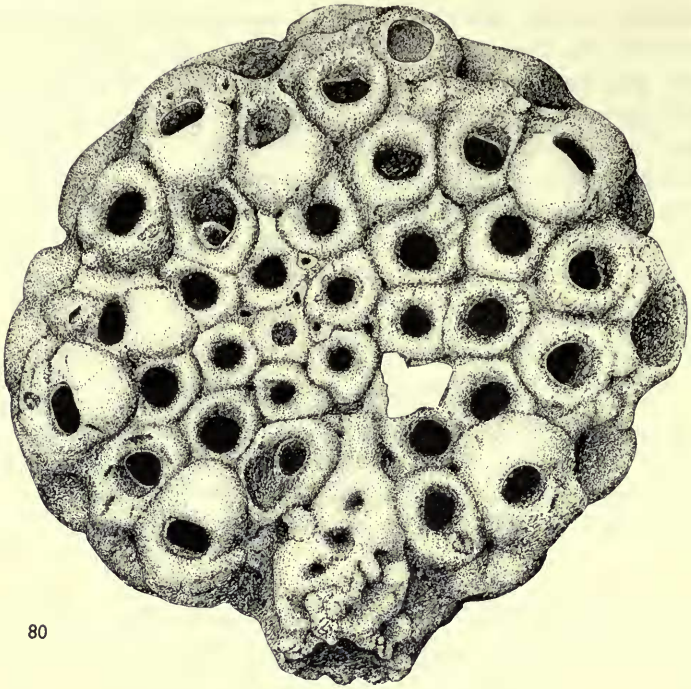
Orbitulipora petiolus (Lonsdale)

(Text-fig. 80)

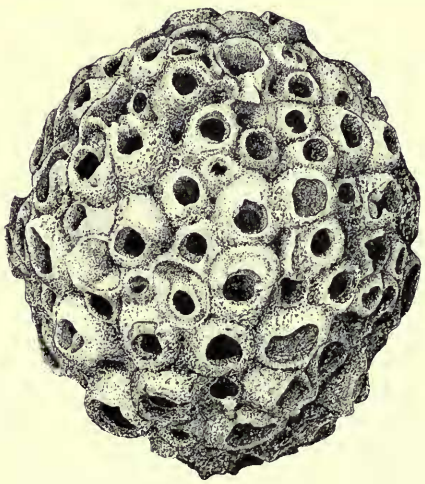
1850 *Cellepora petiolus* Lonsdale : 151.
1854 *Cellepora petiolus* Lonsdale ; Morris : 120.
1862 *Orbitulipora haidingeri* Stoliczka : 91, pl. 3, fig. 5.
1867 *Orbitulipora petiolus* (Lonsdale) Reuss : 217, pl. 1, figs. 1, 2.
1881 *Orbitulipora petiolus* (Lonsdale) ; Mourlon : 180, 191, 202.
1889 *Orbitulipora petiolus* (Lonsdale) ; Vine : 163, pl. 5, fig. 10.
1893 *Biselenaria offa* Gregory : 235, pl. 30, figs. 4, 4*a* (not fig. 5).
1893 *Orbitulipora petiolus* (Lonsdale) ; Gregory : 253, pl. 31, figs. 12–14.
1907*b* *Orbitulipora petiolus* (Lonsdale) ; Canu : 102.
1919 *Orbitulipora petiolus* (Lonsdale) ; Waters : 91.
1926 *Orbitulipora petiolus* (Lonsdale) ; Canu : 758, pl. 30, fig. 5.
1929*a* *Orbitulipora petiolus* (Lonsdale) ; Canu & Bassler : 49.
1929*b* *Orbitulipora petiolus* (Lonsdale) ; Davis : 111.
1931 *Orbitulipora petiolus* (Lonsdale) ; Canu & Bassler : 16, pl. 3, figs. 1–22 ; pl. 4, figs. 1–4.
1933 *Orbitulipora petiolus* (Lonsdale) ; Dartevelle : 108.
1936 *Orbitulipora petiolus* (Lonsdale) ; Dartevelle : 29.
1939 *Orbitulipora petiolus* (Lonsdale) ; Franke : 64, pl. 3, figs. 2*a–d*.
1963 *Orbitulipora petiolus* (Lonsdale) ; Malecki : 137, pl. 15, fig. 5.

FIGURED SPECIMEN. D.48973 (Text-fig. 80).

ADDITIONAL MATERIAL. One hundred and forty-eight specimens, D.48974–D.49073.



80



81

1.00mm

FIGS. 80–81. Fig. 80. *Orbitulipora petiolus* (Lonsdale). D.48973. Lateral view of discoidal zoarium showing well-developed basal peduncle and several ovicelled peripheral zooecia. Fig. 81. *Batopora glandiformis* (Gregory). D.49074. Lateral view of globular zoarium. Three ovicelled zooecia and three vicarious avicularia are visible.

Diagnosis. *Orbitulipora* with discoidal zoarium circular in lateral outline but for the basal peduncle.

Description. *Zoarium* discoidal, flat on both sides, circular in lateral outline save for the basal peduncle. Zooecia arranged in two laminae, their basal walls in contact, those of each lamina in approximate annular arrangement, the largest zooecia at the periphery, the smallest at the centre of the face. Distal margins of zooecia directed towards centre of face. The central zooecia are often covered by randomly oriented, superposed zooecia. Peduncle equal to about four zooecia in size, the exterior irregularly wrinkled and pitted, the interior smooth and hollow, extending nearly to centre of zoarium.

Zooecia irregularly rhombic, pentagonal, or hexagonal, separated by deep grooves. Frontal wall moderately thick, smooth or finely granular, slightly convex, without pores or areolae.

Orifice central, taking up almost the whole frontal surface of zooecium, subcircular, unmodified but buried in thick peristome.

Ovicell hyperstomial, globular, smooth, with distinct distal rim. Orifice of fertile zooecia slightly wider than that of ordinary zooecia. Ovicells developed on zooecia of outer few annulae, on the sides towards the centre of the zoarial face, or on superposed zooecia nearer the centre of the face.

Heterozooecia unknown.

Measurements:

Zoarium

Zoarial height (5) 2·072 (0·5977) mm., 1·26–2·87 mm.
Length of peduncle (5) 0·333 (0·1071) mm., 0·17–0·44 mm.

Ordinary zooecia (at periphery)

Lz (10) 0·345 (0·0380) mm., 0·27–0·38 mm.
lz (10) 0·322 (0·0421) mm., 0·24–0·38 mm.
ho (10) 0·132 (0·0259) mm., 0·09–0·16 mm.
lo (10) 0·153 (0·0142) mm., 0·13–0·17 mm.

Ovicelled zooecia

Lov (6) 0·252 (0·0280) mm., 0·24–0·31 mm.
lo (6) 0·185 (0·0476) mm., 0·17–0·21 mm.

Remarks. In their detailed study of this species, Canu & Bassler (1931 : 16–22) assumed that the centre of the disc-shaped zoarial frond is the ancestrular region, the actual ancestrula lying at the top of the peduncular tube covered by superposed zooecia. The ovicells of the Upper Bracklesham specimens are typical hyperstomial ones, not recumbent as Canu & Bassler (1931 : 17) described them. Avicularia and vibracula are lacking in the Upper Bracklesham specimens ; the structures illustrated by Canu & Bassler as avicularia (1931 : pl. 3, fig. 15) and vibracula (1931 : pl. 3, fig. 21) might be broken ovicells.

As mentioned above (Morphology section, Zoarial Characters), Canu (1931 : 144–147) and Canu & Bassler (1931 : 19–21) supposed *Orbitulipora* to be free-swimming ; Waters (1919 : 90) had earlier suggested the more likely explanation of the peduncle of *Orbitulipora* as a structure for attachment to the substrate.

Silén (1947 : 33) noted that the reversal of the normal proximal-distal relationship in the zoarium of *Orbitulipora* is similar to that in the Conescharellinidae.

Distribution. Eocene (Auversian) ; France, England. Eocene (Auversian, Bartonian) ; Belgium. Eocene (Ludian) ; Poland, ?Italy. Oligocene (Lattorfian) ; Belgium, Germany.

Genus ***BATOPORA*** Reuss

1867 *Batopora* Reuss : 223.
1929*a* *Atactopora* Canu & Bassler : 51, *non* Morren.
1931 *Atactoporidra* Canu & Bassler : 22.

Type species (chosen by Waters 1919). *Batopora stoliczkai* Reuss 1867 : 223, pl. 2, figs. 2–4. Oligocene (Lattorfian) ; Germany.

Diagnosis. Frontal wall calcareous, granular or smooth, without pores or areolae. Orifice sub-circular to semi-circular, with nearly straight proximal margin. Condyles, sinus and ascopore lacking. Whole frontal wall built up round orifice as a kind of peristome. Zoarium spherical, ellipsoidal, discoidal, or conical ; hollow or solid ; the base with a special enlarged pore opening into an axial hollow which runs part way up the zoarium. Zooecia erect, arranged in several laminae, the superficial ones large, with or without ovicells, the deep ones small, without ovicells ; distal margins of zooecia directed apically. Ovicell hyperstomial, globular, smooth.

Remarks. The structure of *Batopora* was studied in detail by Waters (1919) ; the two German Oligocene species, *B. stoliczkai* Reuss and *B. multiradiata* Reuss, considered to be the same by him (1919 : 83, 84), have been re-illustrated by Franke (1939 : pl. 2, figs. 3*a*, *b* ; pl. 3, figs. 1*a*, *b*) as separate species.

Canu & Bassler (1929*a* : 51) established *Atactopora*, later re-named *Atactoporidra*, for Orbituliporids having hollow cylindrical to globular zoaria, differing from *Batopora* which supposedly has conical zoaria. This difference does not seem uniform in the species referred to the two genera, and, furthermore, the type species of *Batopora* has the *Atactoporidra*-type zoarium.

Batopora glandiformis (Gregory)

(Text-fig. 81)

1893 *Heteropora glandiformis* Gregory : 261, pl. 32, fig. 11.
1934 *Atactoporidra glandiformis* (Gregory) Davis : 205.

Holotype. B.4511, Edwards Collection. Barton Beds ; Barton, Hants.

Figured specimen. D.49074 (Text-fig. 81).

Additional material. Twenty-six specimens, D.49075–D.49100.

Diagnosis. *Batopora* with nearly solid, usually spherical zoarium having an inconspicuous basal pit which extends only a short distance up axis; superficial zooecia having large, semi-circular orifices and well-developed ovicells; deep zooecia with much smaller, sub-circular orifices.

Description. *Zoarium* globular, usually spherical, sometimes ellipsoidal or almost discoidal; apical end rounded, basal end slightly more pointed, with a central, circular pit which is inconspicuous and only slightly larger than a zooecial orifice and surrounded by a thin, raised collar. Zooecia arranged irregularly, their distal margins directed towards the apical end of the zoarium. Deep zooecia with only their small orifices showing between larger superficial zooecia.

Zooecia erect, their major axes perpendicular to zoarial surface, with only a small part of the frontal wall, surrounding the orifice, visible frontally. Superficial zooecia protuberant, irregularly polygonal, separated by deep depressions in which orifices of deep zooecia appear. Frontal wall thin, very convex, granular, without pores or areolae.

Orifice of superficial zooecia semi-circular, broadly rounded distally, slightly rounded proximally. Orifice of deep zooecia smaller and sub-circular. Peristome, spines, condyles and sinus all lacking.

Ovicell hyperstomial, small, globular, imperforate, finely granular, present on superficial zooecia only. Orifice of fertile zooecia slightly wider than that of ordinary superficial zooecia.

Avicularia rare, vicarious, about half as large as superficial zooecia, with rounded rostrum and pivotal bar.

Measurements:

Zoarium

Zoarial length (4) 1·706 (0·3086) mm., 1·32–1·96 mm.
Zoarial width (4) 1·511 (0·1812) mm., 1·28–1·71 mm.

Ordinary superficial zooecia

Lz (8) 0·245 (0·0438) mm., 0·19–0·31 mm.
lz (8) 0·239 (0·0333) mm., 0·17–0·27 mm.
ho (8) 0·105 (0·0127) mm., 0·09–0·12 mm.
lo (8) 0·105 (0·0203) mm., 0·09–0·13 mm.

Deep zooecia

ho (4) 0·083 (0·0118) mm., 0·07–0·10 mm.
lo (4) 0·073 (0·0086) mm., 0·07–0·09 mm.

Ovicelled zooecia

Lov (3) 0·125 (0·0131) mm., 0·11–0·14 mm.
lo (3) 0·120 (0·0086) mm., 0·11–0·13 mm.

Avicularia

Lav (2) 0·128 (0·0000) mm., 0·13 mm.

REMARKS. Gregory's (1893) erroneous placing of this species in the Cyclostome genus *Heteropora* was first noted by Waters (1919 : 92) who considered the species a young stage of *Orbitulipora petiolus*. Davis (1934 : 205) recognized the true affinities of the species.

DISTRIBUTION. Eocene (Bartonian) ; England.

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